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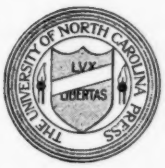

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PEATMOSSES OF THE SOUTHEASTERN STATES

By H. L. Blomquist

Plates 1–5

The peatmosses, or what are botanically known as species of *Sphagnum*, comprise a unique group of plants with more than usual botanical interest. They are commonly classed with the mosses although their structure is quite unlike that of a typical moss.

Aside from their interest to the botanist, they are also of some economic importance. Not being subject to ordinary decay, the dead parts accumulate, especially in colder climates, in deep and extensive deposits. These deposits, which are familiar to everyone as peat, serve in some parts of the world as an important source of fuel. Besides their resistance to decay, due to their antiseptic property, they also have the quality of absorbing and holding large quantities of water. The combination of these two qualities makes them of value in dressing wounds and they have been used for this purpose to some extent, especially in times of war. For the same reason they are often used in packing live plants during transportation. Also in recent years there has been a growing practice of mixing groundup peat with soil to increase the water-holding capacity of the latter.

In view of the fact that peatmosses are interesting and to a certain extent important plants, it is rather surprising how few people in this country have made an attempt to learn to distinguish the different kinds. After devoting some effort to the identification especially of those species occurring in the southeastern states, the author has come to the conclusion that this apparent lack of interest is partly due to the fact that the peatmosses have a traditional reputation of being extremely difficult to identify and partly to the lack of illustrated keys by means of which the characters could be better understood.

The purpose of this paper is, therefore, to present an illustrated key to the peatmosses of the southeastern states with the hope that it will stimulate interest and effort in learning to recognize the different kinds.

In the identification of plants it is of fundamental importance that one has correct notions of the characters referred to in the keys and descriptions. It is also important to have a knowledge of the range of variation exhibited by the characters concerned in order to appreciate their relative taxonomic values. Such facts are acquired only through a morphological study of the plants, including their developmental history. This is especially necessary in a highly specialized group such as *Sphagnum* which is given little or no attention in the general courses in botany and even to a limited extent in the more advanced courses in comparative morphology. It has, therefore, seemed desirable to review in some detail the principal structural features of sphagnum with the hope that by referring to the illustrations the characters can be more easily visualized.

STRUCTURAL CHARACTERISTICS OF SPHAGNUM

As in other mosses, sphagnum has a stem and leaves. In cross section the stem shows two principal regions, a cortex and a central axis (fig. 3). The cortex is composed of one to five layers of hyaline-cells which may (fig. 2) or may not (fig. 45) have fibril-bands and pores similar to those found in the leaves. There is also considerable variation in the size and shape of these cells and the thickness of their walls (figs. 48, 74).

Occasionally the stem forks into two uniform branches (dichotomy), and, as these branches grow indefinitely, they are said to be of unlimited growth (fig. 1). Besides this mode of branching, the stem bears fascicles of branches which are of limited growth. These branches are of two kinds, the spreading or divergent and the slender, drooping (fig. 1). At the summit of the stem the branches are short and crowded forming a tuft called the *capitulum*. The structure of these branches is in general like that of the stem, i.e. with a cortex and a central axis. The cortex of these branches is, however, made up of only one layer of hyaline-cells (fig. 13) which may be uniform (fig. 2) or differentiated into two kinds, large "retort-cells" and smaller cells without pores (fig. 83).

The leaves are composed throughout of one layer of cells in thickness. The cells are of two kinds, large clear or hyaline-cells, devoid of contents except for air or water, and smaller green or chlorophyllose-cells. These two kinds of cells alternate in such a way that the chlorophyllose-cells form a complete network with the hyaline-cells in the meshes (fig. 14).

The hyaline-cells are somewhat cylindrical in cross section and are, at least in the branch-leaves (except in *S. macrophyllum*), provided on the

inside with narrow ring-like or spiral ridges (fibrils) and with pores in the convex free walls (fig. 6) and to some extent between the cells. The margin of these pores may be thin or distinctly thickened. Occasionally the hyaline-cells are divided (fig. 36). Except for the fibril-bands they are commonly smooth on the inside. In some species, however, that part of the wall adjacent to the chlorophyllose-cells is covered with papillae (fig. 34) or ridges (fig. 58).

While there is considerable variation among different species in the arrangement of the fibril-bands, they are of little or no practical taxonomic value. The pores, on the other hand, which vary in number, size, shape, and position in the different species, are often referred to in keys and descriptions (see illustrations).

Besides the regular pores referred to above, there are sometimes irregular openings in the walls of the hyaline cells in the form of eroded gaps which are called "resorbed" areas. These are conspicuous on the outer walls of the cells at and near the apex of the branch-leaves in the species of the subgenus *Inophloea* (fig. 5), as well as in the stem-leaves of this and certain other groups (fig. 35). In some species the hyaline-cells are resorbed on both sides in the stem-leaves, leaving the chlorophyllose-cells loose and, therefore, forming a more or less lacerate leaf (fig. 95).

The chlorophyllose-cells, which are long and narrow, vary considerably in shape in cross section. They may be lenticular, rectangular, trapezoidal, or triangular (see illustrations). They are fairly constant, however, in the different groups, and, therefore, serve as an important taxonomic character.

The relation between the hyaline-cells and the chlorophyllose-cells is likewise of taxonomic importance. This relation is concerned first of all with the location and exposure of the chlorophyllose-cells. In some species they are more or less centrally located between and completely included by the convex walls of the adjacent hyaline-cells (figs. 21, 25). In other species the hyaline-cells include the chlorophyllose-cells on one side only so that the inner or outer walls of the latter are exposed (fig. 59). In still others the chlorophyllose-cells are exposed on both surfaces (fig. 46). Another phase of this relation, which is related to the comparative size of the two kinds of cells, is the extent to which the free convex walls of the hyaline-cells bulge out beyond the chlorophyllose-cells (compare fig. 12 with fig. 89).

Another feature of importance in the leaves concerns the lateral margins. The margin may be composed of a single row of chlorophyl-

lose-cells bordered on the outer edge by a narrow strip of an incomplete hyaline-cell. This narrow strip is known as the "resorption furrow" (figs. 10, 11). In other forms, however, this resorption furrow is absent and the margin is composed of few to several rows of narrow, elongated cells (fig. 75).

In most species of sphagnum there are several types of leaves. The two main types are, of course, the branch- and stem-leaves (figs. 4, 8). The branch-leaves are closely imbricated while the stem-leaves are usually some distance apart. They are commonly quite unlike in size, shape, and structure (*dimorphic*). In exceptional cases, however, as in *S. cyclophyllum* and *S. Pylasii*, the leaves on the stem and branches are regularly quite uniform (*isophyllous*). Isophylly may occasionally appear in varying degrees in almost any species, but it is more common in some than in others. A tendency toward this condition is known as *hemi-isophylly*.

Other types of leaves are those which subtend or surround the reproductive organs, the antheridia and archegonia. In the case of the antheridia (*perigonial-leaves*), these leaves are not essentially different from the ordinary branch-leaves except occasionally they are more deeply pigmented. The *perichaetial-leaves*, i.e., those surrounding the archegonia, are, on the other hand, quite unlike the other leaves.

The antheridia are borne in the axils of the perigonial-leaves on special branches at the base of the capitulum. When these branches are highly colored, which is often the case, they are quite conspicuous and, hence, easily located. The archegonia are borne at the tip of short branches near the center of the capitulum and in order to find them it is necessary first to locate the perichaetial-leaves which are usually larger than the other branch-leaves. Sphagnum may be either monoecious or dioecious.

After fertilization and the consequent development of the sporophyte, the tip of the archegonial branch elongates forming a naked stalk or false seta (*pseudopodium*) which elevates the capsule above the perichaetial-leaves. Unlike the true mosses, the capsules and spores in sphagnum are of little or no taxonomic significance. This is rather fortunate as the plants are not often in fruit when collected.

SYSTEMATICS

Taxonomically the peatmosses have been a difficult group to the botanists. This is due in part to the fact that the characters upon which the keys and descriptions are based are mostly microscopic and somewhat difficult to recognize. Sphagnum is, however, not unique in this

respect as many other plant groups are distinguished by equally obscure characters which, in order to see and understand them, require considerable experience.

The real difficulty of identification, however, has been due to the enormous variation exhibited by the plants themselves and to the selection of some characters for the delimitation of species which intergrade too much to be of any value. This has led to much general confusion and disagreement among students of peatmosses. Opinion has varied from the one extreme of placing all forms of sphagnum into one species to the other extreme of making a large number of species and many varieties. Concerning the questions of phylogeny there has also been considerable disagreement.

So far as the North American species are concerned—and these include the majority of the peatmosses of the world—much of the confusion in taxonomy and phylogeny has been cleared up in the classical treatment by A. LeRoy Andrews.[1] With a conservative viewpoint and a broad concept of species, Andrews has, after a careful study of a wide range of material, reduced a large number of species to synonymy and limited the varieties to only a few.

In the study of peatmosses it has long been recognized that they fall naturally into groups and subgroups. This has been discussed fully by Andrews in a series of papers entitled "Notes on the North American Sphagnum."[2] The characters upon which these subdivisions are based will be briefly reviewed.

Following the concepts and terms of Russow,[3] Andrews divides the species of *Sphagnum* into two groups: I. *Inophloea* (fibrillose cortex) and II. *Litophloea* (smooth or non-fibrillose cortex). These categories are considered as subgenera and, since the two groups are sharply distinct, the suggestion is made that they might ultimately be elevated to generic rank.

SUBGENUS INOPHLOEA

The most conspicuous character of the subgenus *Inophloea* is the presence of spiral-fibrils in the cortical-cells of the stem and branches and the uniformity of these cells (fig. 2). Other characters correlated with this one are: (1) the cucculate apex of the branch-leaves in which the outer surface is roughened due to the erosion ("resorption") of the

[1] North American Flora **15**, Pt. 1: 1-31. 1913.

[2] The Bryologist **14**: 72-75, 1911; **15**: 1-7, 70-74, 1912; **16**: 20-24, 59-62, 74-76, 1913; **18**: 1-6, 1915; **20**: 84-89, 1917; **22**: 45-49, 1919; **24**: 81-86, 1921.

[3] Zur Anatomie der Torfmoose, p. 27 f., Dorpat, 1887.

outer walls of the hyaline-cells (figs. 4, 5); (2) the undifferentiated leaf margin with the presence of a resorption furrow (figs. 10, 11); (3) a uniform narrowing of the hyaline-cells at the base of the stem-leaves; (4) the transformation of the hyaline-cells of the perichaetial-leaves into uniformly long, narrow cells only in the basal and middle portion of the leaf; and (5) the resorption of the outer wall of the hyaline-cells of the stem leaves (figs. 9, 35), although this character is not confined exclusively to this group.

All of the species of this subgenus found in North America are represented in our area.

SUBGENUS LITOPHLOEA

In contrast to *Inophloea*, the second subgenus *Litophloea* is characterized by the absence of spiral-fibrils in the cortical-cells. Other characters correlated with these are: (1) apex of branch-leaves straight or only slightly cucculate, usually toothed and smooth on the back (figs. 40, 41); (3) leaf margin highly differentiated, consisting of several rows of narrow, elongated cells (fig. 75); (3) a tendency to suppression of the hyaline-cells in the basal region of the stem-leaves together with a differentiation of a distinct border of several rows of narrow cells (fig. 82); and (4) the transformation of the hyaline-cells in the perichaetial-leaves into uniformly long and narrow cells in the basal, lateral, and apical regions. The resorption of the hyaline-cell walls of the stem-leaves alternates from the outer to the inner side in the different groups.

Litophloea is the larger of the two subgenera. Since most of the species which comprise it have northern affinities it is not as well represented in the southeastern states as *Inophloea*.

The species of the subgenus *Litophloea* fall naturally into several groups and subgroups, and Andrews has adopted the following classification:

SECTION MALACOSPHAGNUM

This is considered as a transition group between the *Inophloea* and *Litophloea* since the species comprising it show some resemblances to both subgenera. The cortical-cells are without fibrils but are all of the retort type (fig. 22), which distinguishes this section from the other sections of the subgenus. The margin of the branch-leaves shows a resorption furrow as in *Inophloea*, but the stem-leaves have a differentiated border typical of *Litophloea*.

The two species found in North America which belong to the section *Malacosphagnum* occur in our area.

SECTION ACISPHAGNUM

The characters common to the species of this section are more typical of the subgenus *Litophloea*. The section has been divided into the following "groups:" *Squarrosa*, *Cuspidata*, *Acutifolia*. These groups are separated mainly on the basis of the location of the resorption gaps in the hyaline-cells of the stem- and perichaetial-leaves.

In the *Squarrosa* group, the outer membrane of the hyaline-cells of both stem- and perichaetial-leaves is resorbed as in *Inophloea*, while in the other two groups resorption occurs on the inner side of the stem-leaves. In the *Cuspidata* group, resorption takes place on the inner side of the perichaetial-leaves but is entirely absent in the *Acutifolia*. In some species of the *Cuspidata* and *Acutifolia* groups resorption may take place to a certain extent on both surfaces of the stem-leaves, giving the leaf a conspicuously lacerate appearance which, being easily observed, is a convenient diagnostic character. Other practical diagnostic characters of these groups are, the shape and exposure of the chlorophyllose-cells of branch-leaves, the character of the cortical-cells of the stem, and the size and shape of the stem-leaves. Furthermore the pigment of the *Cuspidata* group is brown, while that of the *Acutifolia* group is usually red. The practical value of this character is questionable, however, since there is considerable variation in the degree of pigmentation even to the extent that it may be absent altogether.

As the *Squarrosa* group is typically northern in its distribution, it barely reaches the southeastern states. The only species present is *S. squarrosum* which reaches its southern limit in western North Carolina and eastern Tennessee.

The *Cuspidata* group, on the other hand, is well represented with seven species, some of which, such as *S. Fitzgeraldi*, *S. macrophyllum* and *S. cyclophyllum*, are more or less southern in their distribution.

Although the *Acutifolia* group may in general be said to be composed largely of northern peatmosses, it is represented in the southeastern states by six species. One of these, *S. meridense*, is exclusively tropical.

In the consideration of phylogeny in *Sphagnum*, as in other plants, the relative position of the various categories is determined by the degree of differentiation or specialization. Uniformity of cell structure should, therefore, indicate a primitive position. This is illustrated by the subgenus *Inophloea* in which the cortical cells of the branches are not only uniform but are, like the hyaline-cells of the branch-leaves, also provided with spiral-fibrils. Correlated with this uniformity is the low degree of differentiation of the leaf margin. *Litophloea*, on the

other hand, shows a higher degree of differentiation in the absence of fibrils from the cortical-cells, and especially in the fact that two kinds of cells are present in the cortex of the branches. These characters, together with a highly differentiated leaf margin, place this group higher in the scale of evolution than *Inophoea*.

The included chlorophyllose-cell (fig. 21) is a primitive character but, since this occurs in the various groups, it cannot be considered of major phylogenetic importance.

According to the above concepts and interpretation of facts, the classification of the species of *Sphagnum* which have been found to occur in the southeastern states may be outlined as follows:

Subgenus I. Inophloea
S. magellanicum
S. papillosum
S. erythrocalyx
S. palustre
S. henryense
S. imbricatum
S. portoricense
Subgenus II. Litophloea
Section I. Malacosphagnum
S. compactum
S. strictum
Section II. Acisphagnum
Group a. Squarrosa
S. squarrosum
Group b. Cuspidata
S. recurvum
S. cuspidatum
S. Fitzgeraldi
S. subsecundum
S. Pylaesii
S. cyclophyllum
S. macrophyllum
Group c. Acutifolia
S. Girgensohnii
S. capillaceum
S. quinquefarium
S. meridense
S. tenerum
S. tabulare

The specimens upon which this report is based are mainly the collections in the Duke University Herbarium from North and South Carolina,

Georgia, Florida, Alabama, Mississippi, and eastern Tennessee. The key may no doubt be used, however, in the other states south of the Mason Dixon Line east of the Mississippi River.

TECHNIQUE

In the use of the following key it might be helpful to add a few remarks concerning the technique in making the necessary analysis.

For the examination of most details, the material should be moist. The cortical-cells of the branches may be examined after the removal of the leaves by means of a scalpel or a needle. In examining the stem or the stem-leaves, the fascicles of branches should be removed from the stem. The cortex and leaves may be viewed from the surface but, due to the opaqueness of the central region, it is best to scrape off some of the cortex and leaves. To determine the number of layers of cortical-cells it is necessary to make a thin section of the stem with a sharp scalpel or razor blade under a binocular microscope or in pith.

In the examination of leaves it is necessary to select a *typical* leaf. This is not difficult in stem-leaves except in hemi-isophyllous forms. The branch-leaves vary considerably from base to apex and it is, therefore, best to select a leaf from the plumpest part of the branch which is usually about its middle portion. The sectioning of leaves may be done freehand under a binocular or in pith. In slender forms with small leaves, satisfactory sections can usually be obtained by sectioning the branch with the leaves intact. In more robust forms individual leaves may be sectioned successfully. The advantage of sectioning an individual leaf is that the desired (median) section can then be obtained at will instead of by chance. The purpose of sectioning leaves is to obtain a view of the shape of the cells, especially the chlorophyllose-cells, and to determine the position of the resorption gaps. With some experience a considerable amount of sectioning may be dispensed with as one soon learns to interpret the shape and exposure of cells and the presence and position of resorption gaps from surface views (consult the illustrations). In order that certain features, such as pores and resorbed areas, can be more easily observed, it is often advantageous to use dyes, such as methyline blue, safranin, or gentian violet. In examining the hyaline leaf cells for pores, it should be borne in mind that these vary to a great extent throughout the leaf and that reference is usually made to the cells in the middle of the leaf.

KEY TO SPECIES AND VARIETIES[4]

1a. Cortical-cells of the stem and branches uniform with fibril-bands (2)[5]; apex of branch leaves cucullate (4) with the outer hyaline-cells conspicuously eroded (5); resorption furrow present (10, 11).

2a. Chlorophyllose-cells of branch-leaves entirely included (25) or exposed about equally on both surfaces of the leaf (20, 34), narrowly rectangular to lenticular in section.

3a. Chlorophyllose-cells entirely included, half way between both surfaces, short-lenticular in section (25).....1. *S. magellanicum*

3b. Chlorophyllose-cells exposed about equally on both surfaces, narrowly rectangular to lenticular in section.

4a. That part of the wall of the hyaline-cells adjacent to the chlorophyllose-cells papillose (34); chlorophyllose-cells truncately elliptic in section (34).....2. *S. papillosum*

4b. That part of the wall of the hyaline cells adjacent to the chlorophyllose-cells not papillose; chlorophyllose-cells narrowly rectangular in section (20).....3. *S. erythrocalyx*

2b. Chlorophyllose-cells of branch-leaves exposed more broadly on the inner surface of the leaf, triangular to rounded-triangular in section (12, 59).

5a. Chlorophyllose-cells of the branch-leaves isosceles-triangular in section; walls of median hyaline-cells with few or no pores on the inner side of the leaf (7, 16).

6a. That part of the wall of the hyaline-cells of branch-leaves adjacent to chlorophyllose-cells smooth
4. *S. palustre*

6b. That part of the wall of the hyaline-cells of the branch-leaves adjacent to chlorophyllose-cells with an irregular network of longitudinal ridges (15), especially at the base of the leaf...5. *S. henryense*

5b. Chlorophyllose-cells of branch-leaves equilateral-triangular in section (31); the median hyaline-cells with several pores on the inner side of the leaf (57).

7a. Cortical-cells of the branches with the end-walls straight (2), not funnel-shaped.

8a. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells with conspicuous comb-like ridges (58), especially at the base of the leaf.....6. *S. imbricatum*

8b. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells without ridges
6a. *S. imbricatum* v. *affine*

7b. Cortical-cells of the branches with funnel-shaped ends (30).....7. *S. portoricense*

1b. Cortical-cells of the stem and branches without fibril-bands, those of the branches uniform (22) or of two kinds (45, 83); apex of branch-leaves little or not at all cucullate (87, 99), usually toothed (40), hyaline-cells not eroded on the outside; resorption furrow present or absent, when absent the border consisting of a row of few narrow elongated hyaline-cells (75).

---

[4] This key has been adapted to a great extent from Andrew's key to the species of *Sphagnum* of North America (Ibid.). This as well as his *Notes on American Sphagnum* (Ibid.) should be consulted for more detailed descriptions.

[5] The numbers refer to the figures.

9a. Resorption furrow present in the branch-leaves; cortical-cells of the branches more or less uniform, each with a pore at the upper end (22).
10a. Chlorophyllose-cells completely included, closer to the outer surface, elliptic in section (21).....8. *S. compactum*
10b. Chlorophyllose-cells exposed on the outer surface, rounded-triangular in section (61).....9. *S. strictum*
9b. Resorption furrow absent (75), cortical-cells of the branches of two kinds, the large retort cells and the smaller cells without pores (83), or, if uniform, all without pores.
11a. Chlorophyllose-cells of the branch-leaves triangular (68A) to trapezoidal (37) or rounded-rectangular (46), *exposed more broadly on the outer surface.*
12a. Chlorophyllose-cells triangular in section and exposed on the outer surface (68A).
13a. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells papillose (68A); stem-leaves somewhat fimbriate at the broad apex; branch-leaves usually conspicuously squarrose (66) 10. *S. squarrosum*
13b. That part of the wall of the hyaline-cells of the branch leaves adjacent to the chlorophyllose-cells not papillose; stem-leaves not fimbriate at the usually narrow and toothed apex (40).
14a. *Branch-leaves, when dry, with spreading and usually twisted tips* (69); cortical-cells of the stem uniform, small, thick-walled and without pores (72, 74) 11. *S. recurvum*
14b. *Branch-leaves, when dry, not with spreading or twisted tips* (41); cortical-cells of the stem larger, thin-walled (47, 48), at least some with pores.
15a. Branch-leaves lanceolate to long-lanceolate (41), *not serrulate on the margin;* plants not delicate.
16a. Branch-leaves not undulate when dry; plants not always submerged aquatic 12. *S. cuspidatum*
16b. Branch-leaves undulate when dry; plants more robust, usually submerged 12a. *S. cuspidatum* v. *Torreyi*
15b. Branch-leaves mostly linear-lanceolate, *serrulate on the margin by the projecting ends of the border cells* (42), plants delicate, always aquatic.....12b. *S. cuspidatum* v. *serrulatum*
12b. Chlorophyllose-cells of branch-leaves in section from trapezoidal (37) with broader exposure on the outer surface to rectangular or rounded-rectangular with equal exposure on both surfaces (46, 56).
17a. Hyaline cells of the branch-leaves without fibril-bands, long and narrow, with a single row of pores in the middle of the outer wall (54) 17. *S. macrophyllum*
17b. Hyaline-cells of the branch-leaves with fibril-bands, not with a single central row of pores.

18a. Chlorophyllose-cells in section triangular-trapezoidal *with lumen triangular* (37); branch-leaves not strongly concave when dry (41, 42, 60).

19a. Branch-leaves short- to long-lanceolate or linear-lanceolate; *stem-leaves usually small, not hemi-isophyllous;* plants greenish

12. *S. cuspidatum* and varieties (see above)

19b. Branch-leaves short-ovate to oblong or nearly quadrate (60); *stem-leaves large, hemi-isophyllous;* plants delicate and whitish

13. *S. Fitzgeraldi*

18b. Chlorophyllose-cells in section trapezoidal with broader exposure on the outer surface to rectangular or rounded-rectangular with about equal exposure on both surfaces, *the lumen trapezoidal, rectangular or lenticular;* branch-leaves strongly concave when dry.

20a. *Plants with typical fascicles of branches* (1); *leaves ovate to ovate-lanceolate, usually not isophyllous;* chlorophyllose-cells of branch-leaves rounded-rectangular to truncately elliptic in section and exposed about equally on both surfaces, or broadly trapezoidal and exposed more broadly on the outer surface.

21a. Chlorophyllose-cells of branch-leaves truncately elliptic in section, the lumen lenticular (84); *outer walls of hyaline cells of branch-leaves with a few large pores or none, the inner walls with several large pores in different parts of the wall* (85, 86); branch-leaves deeply concave, *abruptly involute-acuminate* (87); *plants exclusively tropical*.....21. *S. meridense*

21b. Chlorophyllose-cells of branch-leaves rounded-rectangular, exposed equally on both surfaces, to broadly trapezoidal and exposed more broadly on the outer surface; *outer walls of hyaline-cells typically with numerous small, elliptic strongly ringed pores in bead-like rows along the sutures* (44), at least in the upper part of the leaf, the inner walls with few or no pores (43); branch-leaves gradually involute-acuminate to acute (41); plants not exclusively tropical

14. *S. subsecundum*

20b. Plants without typical fascicles of branches (49, 50); *leaves almost orbicular* (52); *isophyllous* (49, 50); chlorophyllose-cells of branch-leaves rectangular in section and exposed equally on both surfaces (56).

22a. Plants short, sparingly branched (49, 50), plump, brown in color, *growing at low altitudes;* pores on the outer surface of the hyaline-cells more than 2 per cell

15. *P. cyclophyllum*

22b. Plants longer, more branched, slender, dark-brown to black, *growing at high altitudes;* pores when present not more than 2 per cell.....16. *P. Pylaesii*

11b. Chlorophyllose-cells of the branch-leaves triangular to trapezoidal in section, *exposed more broadly on the inner surface.*

23a. *Plants without typical fascicles of branches* (49, 50); color brown to black; leaves almost orbicular (52), isophyllous (49, 50); chlorophyllose-cells trapezoidal in section

P. cyclophyllum and *P. Pylaesii* (see above)

23b. *Plants with typical fascicles of branches* (1), color, if any, red; leaves not orbicular nor isophyllous; chlorophyllose-cells triangular to trapezoidal in section.

24a. Stem-leaves conspicuously fimbriate-lacerate (95) at the broad apex
18. *S. Girgensohnii*

24b. Stem-leaves not fimbriate-lacerate at the apex, often toothed.

25a. Hyaline-cells of the branch-leaves in proportion to the chlorophyllose-cells large in section (89, 96), *their free convexity on the outer surface usually more than half their diameter*, strongly convex on the inner surface (89, 96).

26a. *Upper margin of the branch leaves not denticulate;* chlorophyllose-cells in proportion to the hyaline-cells very small, usually exposed on both surfaces (89); hyaline-cells strongly convex on the inner surface; plants commonly not short and stout; stem-leaves usually not hemi-isophyllous ..... 22. *S. tenerum*

26b. *Upper margin of the branch leaves denticulate* (99); chlorophyllose-cells not very small (96), usually exposed only on the inner surface; hyaline-cells not strongly convex on the inner surface (96); plants commonly short and stout; stem-leaves often hemi-isophyllous
23. *S. tabulare*

25b. Hyaline-cells of the branch-leaves in proportion to the chlorophyllose-cells smaller in section, *their free convexity on the outer surface usually less than half their diameter* (81), little convex on the inner surface (78, 81).

27a. *Branch-leaves gradually involute-acuminate to acute* (88), outer surface of hyaline-cells with several large pores; plants not exclusively tropical.

28a. *Stem-leaves large*, lingulate to lingulate-ovate, one and one-half or more as long as wide (80); hyaline-cells with some free convexity on the inner surface.

29a. Stem leaves narrowly lingulate to triangular-ovate, *few or no hyaline-cells of stem-leaves divided* (14); plants not slender ..... 19. *S. capillaceum*

29b. Stem leaves broad-lingulate; *hyaline-cells of stem-leaves mostly divided* (36); plants commonly slender
19a. *S. capillaceum* v. *tenellum*

28b. *Stem-leaves smaller, not much longer than wide*, triangular to triangular-lingulate (79); hyaline-cells with little or no free convexity on the inner surface (78)
20. *S. quinquefarium*

27b. Branch-leaves *abruptly involute-acuminate* (87); outer surface of hyaline-cells with few or no pores; *plants exclusively tropical*
21. *S. meridense*

ANNOTATED LIST OF SPECIES AND VARIETIES

1. **Sphagnum magellanicum** Brid. (*S. medium* Limpr., *S. intermedium* Russow.) Figs. 25, 26, 27.

Not common. Distribution general throughout the area.

Often recognized in the field by its reddish color. The only species of the subgenus *Inophloea* with included chlorophyllose-cells; the only other species with included chlorophyllose-cells is *S. compactum* from which it is easily distinguished by its fibrillose cortical-cells.

2. **Sphagnum papillosum** Lindb. Figs. 32, 33, 34.

Rare. Reaching its southern limit in the upper coastal plain of southeastern North Carolina.

Closely related to *S. erythrocalyx* from which it is easily distinguished by its papillose lateral regions of the hyaline leaf-cells and its larger pores on the outer walls of the hyaline-cells. This species has been found most suitable for surgical dressing.

3. **Sphagnum erythrocalyx** Hampe. (*S. guadalupense* Schimp., *S. ludovicianum* Warnst.) Figs. 18, 19, 20.

Common. Coastal plain throughout the area.

Very variable but recognized in the field by its compact form and reddish to brown-blackish color; readily distinguished from *S. palustre* or *S. henryense* by the small pores of the hyaline-cells of the branch-leaves.

4. **Sphagnum palustre** L. (*S. cymbifolium* Ehrh.) Figs. 1–14, 35.

Common at higher altitudes, decreasing in frequency toward the coast. Throughout the area.

This species is sometimes confused with *S. imbricatum* var. *affine* and *S. henryense*. From the former it can be distinguished by the isosceles-triangular chlorophyllose leaf-cells, from the latter by the lack of a network of ridges on the lateral sides of the hyaline leaf-cells.

5. **Sphagnum henryense** Warnst. Figs. 15–17.

Rather rare. Confined to the coastal plain throughout the area.

This species might be confused with *S. palustre* unless one is careful to look for the network of ridges on the lateral sides of the hyaline leaf-cells, and the smaller, strongly ringed pores on the outer surface.

6. **Sphagnum imbricatum** Kornsch. (*S. Austini* Sull.) Figs. 57–59.

Fairly common. Of general distribution throughout the area.

Most easily recognized of all species by the presence of fringe-fibrils on the lateral sides of the hyaline leaf-cells, which are often only evident at the base of the leaf. Not likely to be confused with *S. portoricense* from general appearances and from the lack of funnel-shaped cortical branch-cells characteristic of the latter.

6a. **Sphagnum imbricatum** var. **affine** (Ren. & Card.) Warnst. (*S. affine* Ren. & Card.)

Of about the same frequency and distribution as the species.

7. **Sphagnum portoricense** Hampe. (*S. Sullivantianum* Aust.) Figs. 28–31.

Not common. Confined to the coastal plain; not reported from Alabama, Mississippi, and Louisiana.

Easily recognized in the field by its usual robust form and the club-shaped branches. Most closely related to *S. imbricatum.*

8. **Sphagnum compactum** DC. (*S. rigidum* Schimp.) Figs. 21–24.

Common. Of general distribution throughout the area, although not reported west of Alabama in the Gulf States.

Recognized in the field by its short and compact form which it has, however, in common with *S. strictum* and *S. tabulare.* Not likely to be confused with *S. strictum* because of its included chlorophyllose-cells and *S. tabulare* because of the same character and, in addition, by its uniform cortical-cells of the stem.

9. **Sphagnum strictum** Sull. Figs. 61–63.

Rare in the Carolinas; more frequent southward. Coastal plain, but extending into other sections throughout the area.

10. **Sphagnum squarrosum** Crome. Figs. 66–68.

Rare. Collected in western North Carolina and eastern Tennessee where it reaches the southern limit of its range.

Easily recognized in the field by its squarrose branch-leaves, and microscopically by the papillae on the lateral sides of its hyaline leaf-cells.

11. **Sphagnum recurvum** Beauv. (*S. pulchricoma* C. Mull., *S. riparioides* Warnst.) Figs. 69–75.

Fairly common. Of general distribution throughout the area.

Best recognized macroscopically in dried condition by the twisted recurved tips of the branch leaves. Quite variable and often confused with *S. cuspidatum* from which it is best distinguished by the characters given in the key.

12. **Sphagnum cuspidatum** Ehrh. (*S. virginianum* Warnst., *S. Faxonii* Warnst.) Figs. 37–41, 47.

Fairly common but decreasing southward. Coastal plain, extending into the lower piedmont; not collected west of Georgia in the Gulf States.

Growing in wet places or in water. Highly variable, grading into the following two varieties.

12a. **Sphagnum cuspidatum** var. **Torreyi** (Sull.) Braithw.

Rare. Not collected south of North Carolina.

This resembles to some extent *S. recurvum* in its undulate leaves but typically does not show the twisted or recurved leaf-tips.

12b. **Sphagnum cuspidatum** var. **serrulatum** Schlieph. Fig. 42.

Not common except locally. Near the coast throughout the area.

Very delicate and always growing in water. Easily recognized by the serrulate linear branch-leaves.

13. **Sphagnum Fitzgeraldi** Ren. (*S. Mohrianum* Warnst.) Figs. 60, 64, 65.

Not common. Near the coast from southeastern North Carolina to Florida and Alabama.

Recognized in the field by its delicate whitish appearance; resembling somewhat *S. cuspidatum* var. *serrulatum* but distinguished from it by the ovate to rectangular leaves which are not serrulate on the margin.

14. **Sphagnum subsecundum** Nees. (*S. auriculatum* Schimp., *S. laricinum* Spruce, *S. mobilense* Warnst., *S. orlandense* Warnst., *S. inundatum* Russow., *S. Louisianae* Warnst., etc.) Figs. 43, 46, 48.

Common. Distribution general throughout the area.

This species is extremely variable as is apparent from the extensive synonymy. When typical it is easily recognized by the numerous bead-like pores along the commissures of the hyaline leaf-cells; when these are absent, the shape and exposure of the chlorophyllose-cells and the large cortical-cells of the stem will be sufficient to determine its identity.

15. **Sphagnum Pylaesii** Brid.

Rare. Found only at high altitudes in eastern Tennessee and western South Carolina where it reaches its southern limit of distribution.

This species is closely related to *S. cyclophyllum*, with which it can hardly be confused because of their differences in distribution.

16. **Sphagnum cyclophyllum** Sull. & Lesq. (*S. alabamae* Warnst.) Figs. 51–53.

Not common. Confined to the coastal plain throughout the area.

Easily recognized in the field by its sparcity of branches and the isophyllous almost orbicular leaves.

17. **Sphagnum macrophyllum** Bernh. (*S. floridanum* Card.) Figs. 54–56.

Not common. In the coastal plain throughout the area.

This peculiar species is easily recognized—if recognized as a peatmoss—by its aquatic habitat and its general appearance.

18. **Sphagnum Girgensohnii** Russow. (*S. strictum* Lindb.) Figs. 90–95.

Rare and only at high altitudes. Collected in western North Carolina and eastern Tennessee where it reaches its southern limit of distribution in eastern North America.

In general appearance this species resembles *S. capillaceum* and *S. quinquefarium* and can best be distinguished from these two by the lacerate apex of the stem leaves.

19. **Sphagnum capillaceum** (Weiss.) Schrank. (*S. acutifolium* Ehrh.) Figs. 80–83, 88.

Common. Distribution general throughout the area but less common near the coast.

This is a highly variable species. It is easily confused with *S. quinquefarium* and *S. tenerum*, from which it can best be separated by the characters given in the key.

19a. **Sphagnum capillaceum** var. **tenellum** (Schimp.) A. L. Andrews. (*S. rubellum* Wilson, *S. acutifolium tenellum* Schimp.) Fig. 36.

Not common. At the higher altitudes as far south as western South Carolina.

Usually more slender and with more pigmentation than the species.

20. **Sphagnum quinquefarium** (Lindb.) Warnst. (*S. acutifolium quinquefarium* Lind.) Figs. 76–79.

Not common. Found only at higher altitudes as far south as Georgia.

Distinguished in the field sometimes by the sharply five-angled branches.

21. **Sphagnum meridense** (Hampe) C. Mull. (*S. acutifolium meridense* Hampe.) Figs. 84–87.

This is a tropical species which reaches the extreme southern tip of Florida.

Easily distinguished from the others of the *Acutifolia* group by the scarcity of pores on the outer surface of the hyaline-cells of the branch-leaves.

22. **Sphagnum tenerum** Sull. & Lesq. Fig. 89.

Rare. Collected at higher altitudes as far south as Alabama.

This species is closely related to *S. capillaceum* from which it can best be separated by its large hyaline-cells, strongly convex on both surfaces, and its minute chlorophyllose-cells.

23. **Sphagnum tabulare** Sull. (*S. molle* Sull.) Figs. 96–99.

Fairly common. From the mountains to the coast.

Sometimes recognized in the field by its compact form, its sparcity of branching and by its hemi-isophyllous or isophyllous leaves.

The writer is greatly indebted to A. LeRoy Andrews for help and encouragement in the study of sphagnum. To D. S. Correll he owes grateful acknowledgment for the majority of the specimens upon which this paper is based. In the preparation of the manuscript, Lewis E. Anderson has been of invaluable assistance in his criticisms and helpful suggestions.

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EXPLANATION OF PLATES

All figures except 1, 49, 50, and 55, were drawn with the aid of an Abbe camera lucida. All sections of leaves have been drawn with the inner side up.

PLATE 1

1–14. *Sphagnum palustre*

1. Habit of plant, × 1.
2. Surface view of cortical-cells, × 44.
3. Transverse section of stem, × 44.
4. Branch-leaf, × 22.
5. Apex of branch-leaf, × 235.
6. Outer side of cells of branch-leaf, × 235.
7. Inner side of cells of branch-leaf, × 235.
8. Stem-leaf, × 22.
9. Cells in section of stem-leaf, × 235.
10. Cells in section of edge of branch-leaf, × 235.
11. Surface view of edge of branch-leaf, × 235.
12. Cells in section of branch-leaf, × 235.
13. Transverse section of branch, × 44.
14. Surface view of cells of branch leaf, × 235.

15–17. *Sphagnum henryense*

15. Outer side of cells of branch-leaf, × 235.
16. Inner side of cells of branch-leaf, × 235.
17. Cells in section of branch-leaf, × 235.

PLATE 2

18–20. *Sphagnum erythrocalyx*

18. Inner side of cells of branch-leaf, × 235.
19. Outer side of cells of branch-leaf, × 235.
20. Cells in section of branch-leaf, × 235.

21–24. *Sphagnum compactum*

21. Cells in section of branch-leaf, × 235.
22. Surface view of cortex of branch, × 44.
23. Outer side of cells of branch-leaf, × 235.
24. Inner side of cell of branch-leaf, × 235.

25–27. *Sphagnum magellanicum*

25. Cells in section of branch-leaf, × 235.
26. Inner side of cell of branch-leaf, × 235.
27. Outer side of cell of branch-leaf, × 235.

28–31. *Sphagnum portoricense*

28. Outer side of cell of branch-leaf, × 235.
29. Inner side of cell of branch-leaf, × 235.
30. Surface view of cortex of branch, × 235.
31. Cells in section of branch leaf, × 235.

32–34. *Sphagnum papillosum*

32. Inner side of cells in branch-leaf, × 235.
33. Outer side of cells in branch-leaf, × 235.
34. Cells in section of branch-leaf, × 235.

35. Resorption gaps on outer side of stem-leaf in *S. palustre*, × 235.
36. Divided hyaline-cells in stem-leaf of *S. capillaceum* v. *tenellum*, × 235.

PLATE 3

37–41. *Sphagnum cuspidatum*

37. Cells in section of branch-leaf, × 235.
38. Inner side of cells of branch-leaf, × 235.
39. Outer side of cells of branch-leaf, × 235.
40. Apex of branch-leaf, × 44.
41. Branch-leaf, × 22.
42. Tip of branch-leaf of *S. cuspidatum* v. *serrulatum*, × 64.

43–46. *Sphagnum subsecundum*

43. Inner side of cells in branch-leaf, × 235.
44. Outer side of cells in branch-leaf, × 235.
45. Surface view of cortex of branch, × 44.
46. Cells in section of branch-leaf, × 235.

47. Section of outer region of stem of *S. cuspidatum*, × 235
48. Section of outer region of stem of *S. subsecundum*, × 235.

49–53A. *Sphagnum cyclophyllum*

49, 50. Habit of plants, × 2.
51. Cells in section of branch-leaf, × 235.

52. Branch-leaf, × 44.
53. Inner side of cells of branch-leaf, × 235.
53A. Outer side of cells of branch-leaf, × 235.

54–56. *Sphagnum macrophyllum*

54. Outer side of cells of branch-leaf, × 235.
55. Habit of plant, × 1.
56. Cells in section of branch-leaf, × 235.

PLATE 4

57–59. *Sphagnum imbricatum*

57. Inner side of cells of branch-leaf, × 235.
58. Outer side of cells of branch-leaf, × 235.
59. Cells in section of branch-leaf, × 235.

60. Upper branch-leaf of *S. Fitzgeraldi*, × 44.

61–63. *Sphagnum strictum*

61. Cells in section of branch-leaf, × 235.
62. Inner side of cells of branch-leaf, × 235.
63. Outer side of cells of branch-leaf, × 235.

64–65. *Sphagnum Fitzgeraldi*

64. Inner side of cells of branch-leaf, × 235.
65. Outer side of cells of branch-leaf, × 235.

66–68A. *Sphagnum squarrosum*

66. Branch leaf, × 44.
67. Cells in section of stem-leaf, × 235.
67A. Inner side of cells of branch-leaf, × 235.
68. Outer side of cells of branch-leaf, × 235.
68A. Cells in section of branch-leaf, × 235.

69–75. *Sphagnum recurvum*

69. Branch-leaf, × 44.
70. Inner side of cells of branch-leaf, × 235.
71. Outer side of cells of branch-leaf, × 235.
72. Surface view of cortex-cells of stem, × 235.
73. Cells in section of branch-leaf, × 235.
74. Section of outer region of stem, × 235.
75. Surface view of border of branch-leaf, × 235.

PLATE 5

76–79. *Sphagnum quinquefarium*

76. Outer side of cells of branch-leaf, × 235.
77. Inner side of cells of branch-leaf, × 235.

78. Cells in section of branch-leaf, × 235.
79. Stem leaf, × 44.

80-83. *Sphagnum capillaceum*

80. Stem leaf, × 44.
81. Cells in section of branch-leaf, × 235.
82. Lower marginal cells of stem-leaf, × 235.
83. Cortical cells of branch, × 44.

84-87. *Sphagnum meridense*

84. Cells in section of branch-leaf, × 235.
85. Outer side of cells of branch-leaf, × 235.
86. Inner side of cells of branch-leaf, × 235.
87. Branch-leaf, × 44.

88. Branch leaf of *S. capillaceum*, × 44.
89. Cells in section of branch-leaf of *S. tenerum*, × 235.

90, 93-95. *Sphagnum Girgensohni*

90. Inner side of cells of branch-leaf, × 235.
93. Outer side of cells of branch-leaf, × 235.
94. Cells in section of branch-leaf, × 235.
95. Apex of stem-leaf, × 44.

96-99. *Sphagnum tabulare*

96. Cells in section of branch-leaf, × 235.
97. Outer side of cells of branch-leaf, × 235.
98. Inner side of cells of branch-leaf, × 235.
99. Apex of branch-leaf, × 44.

PLATE 1

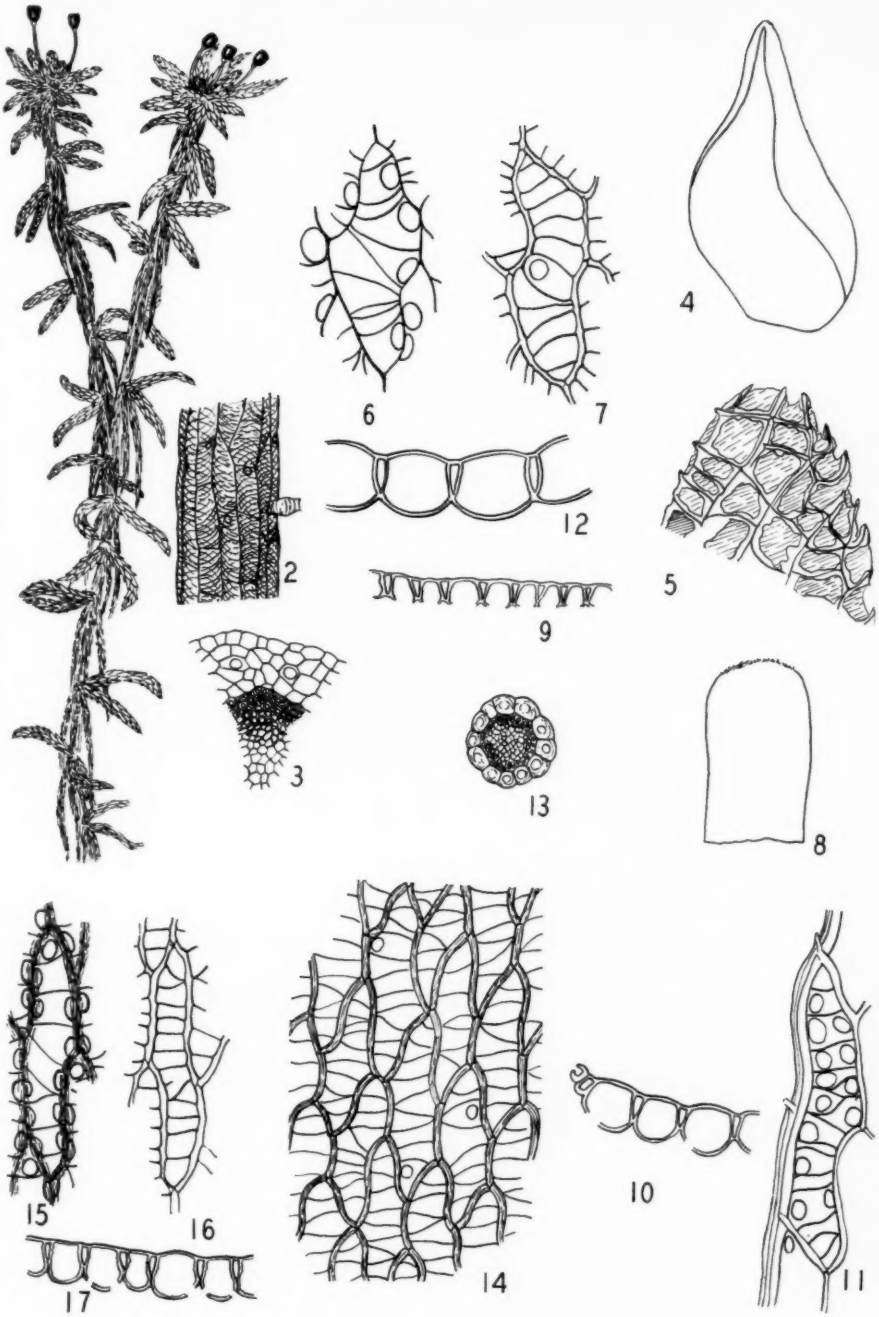

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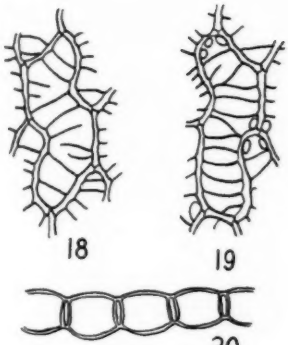
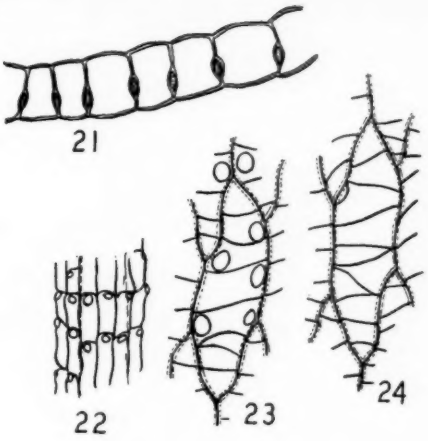
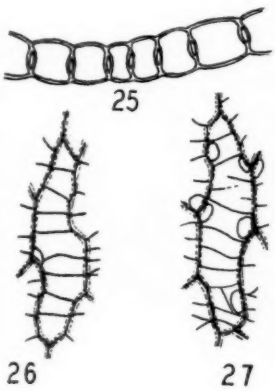
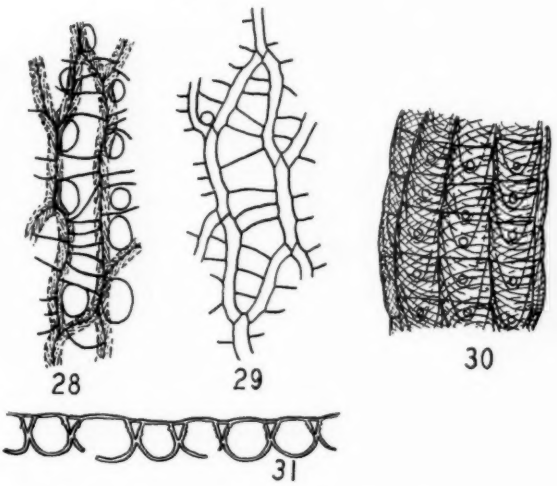
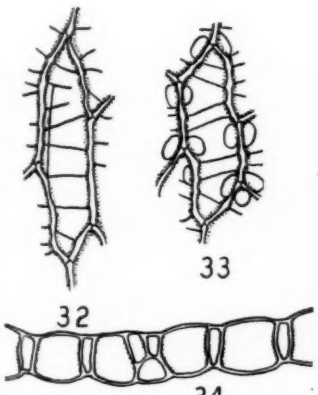
PLATE 2











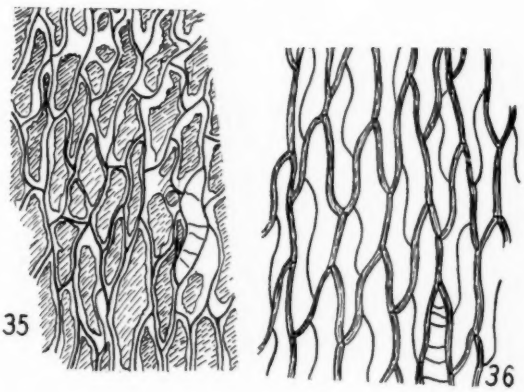


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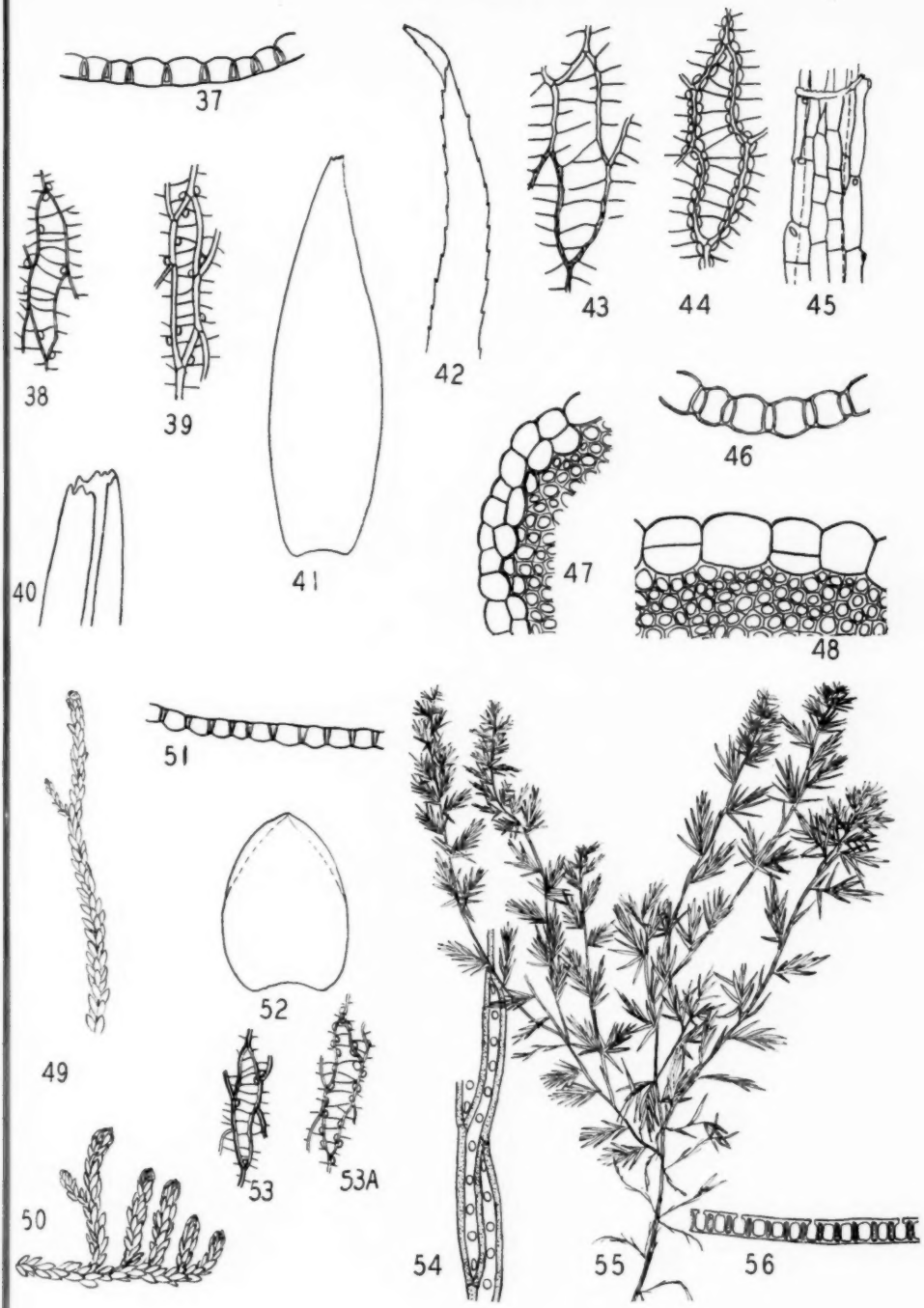
PLATE 3



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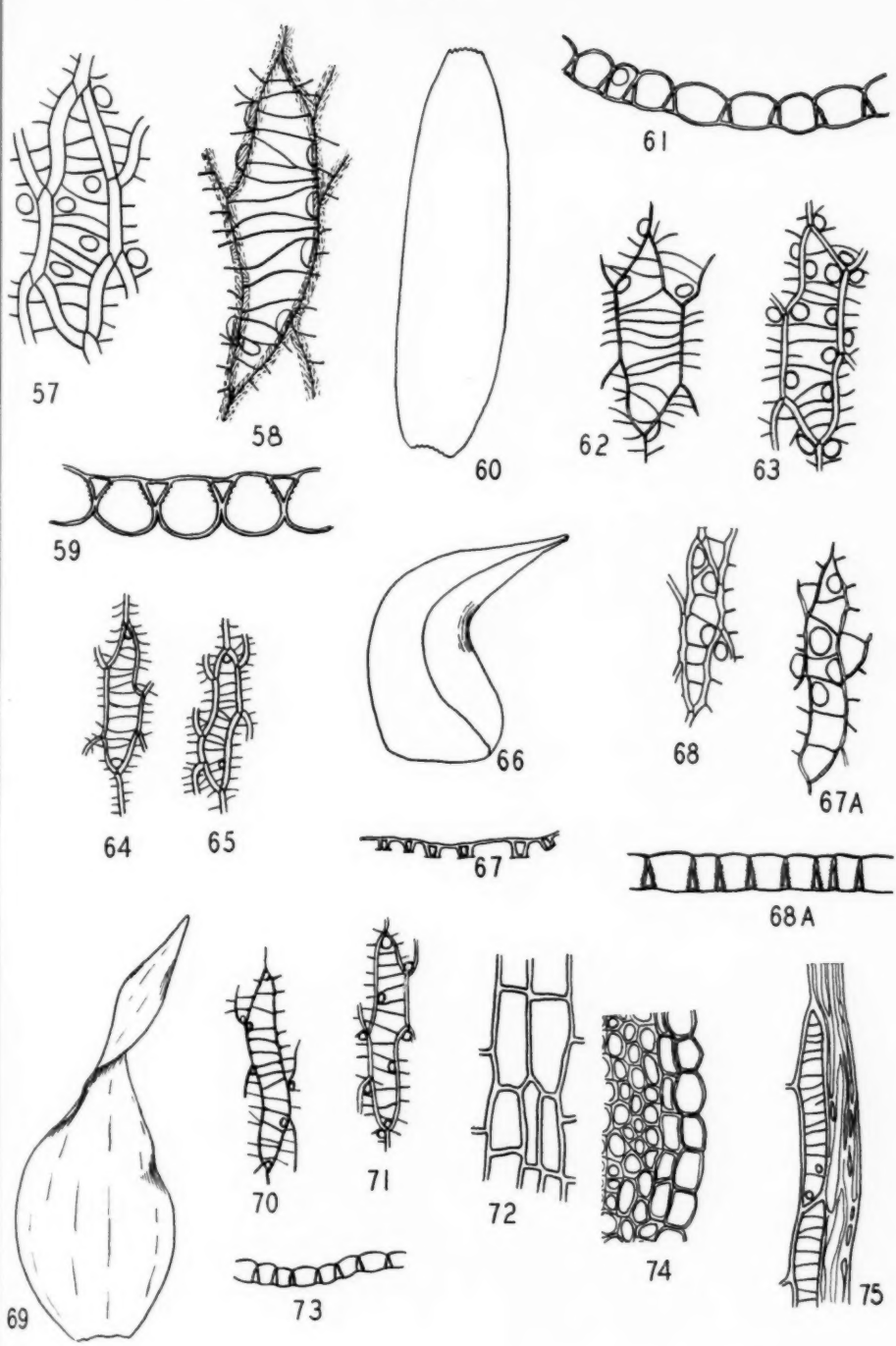

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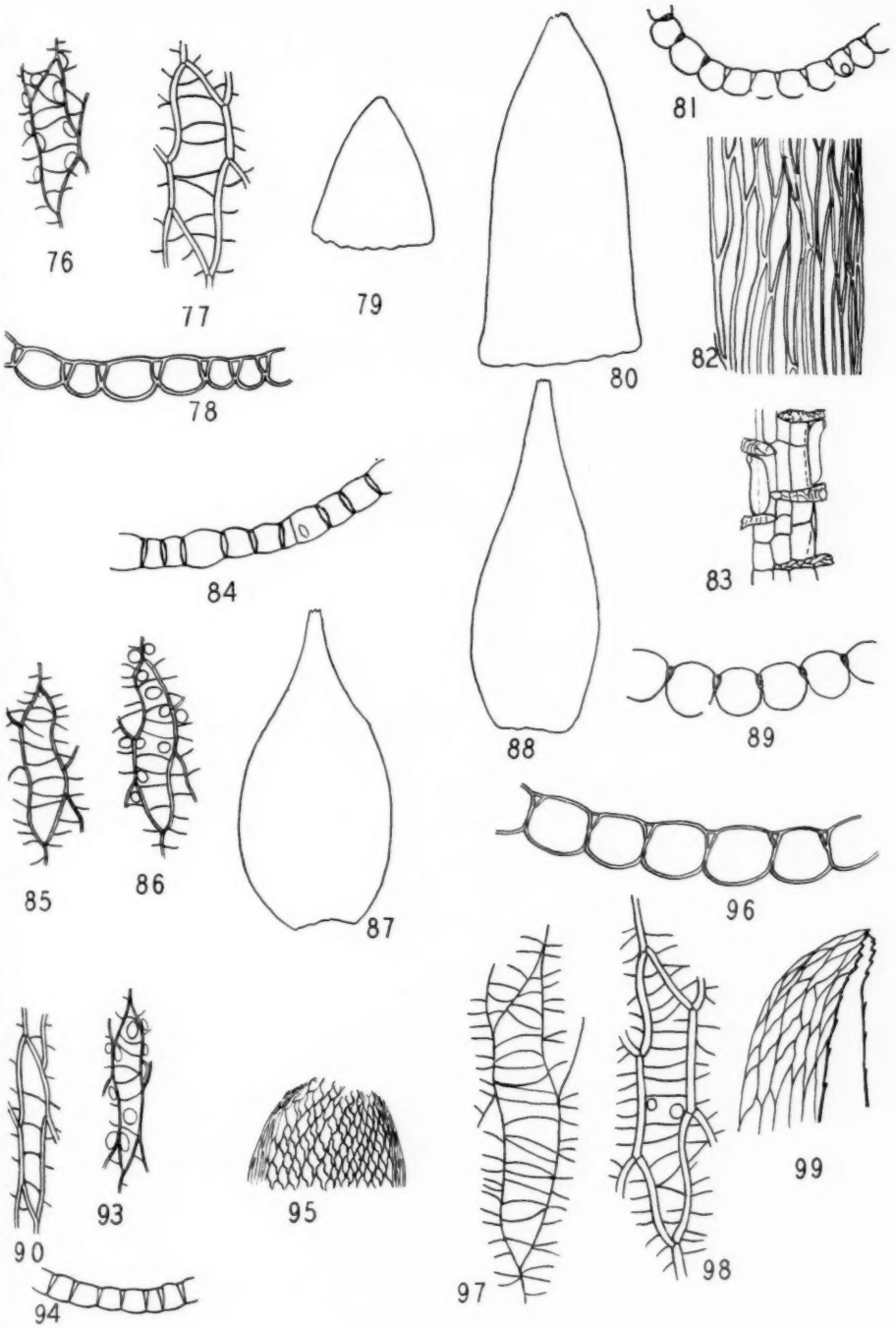

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THE CLASSIFICATION OF CORRELATIONS IN SPACE

By E. T. Browne

1. *Introduction.* A correlation in space is a projective correspondence between the points and the planes of space such that all the planes through a point correspond to all the points on a plane. Analytically, a correlation in space is defined by equations of the type

$$\rho u_i = \Sigma a_{ij} x_j, \qquad (i = 1, \cdots, 4;\ \Delta = |\, a_{ij} \,| \neq 0), \tag{1}$$

where (x_1, x_2, x_3, x_4) are the homogeneous coördinates of a point x, (u_1, u_2, u_3, u_4) are the coördinates of the corresponding plane u, and the frame of reference is thought of as being so chosen that the condition for united position of u and x is

$$\Sigma u_i x_i = 0.$$

On solving the equations (1) for the x's in terms of the u's, we have

$$\sigma x_i = \Sigma A_{ji} u_j \qquad (i = 1, \cdots, 4), \tag{1'}$$

where A_{ij} is the cofactor of a_{ij} in the determinant Δ. The equations (1') serve also to determine the correlation.

Suppose now that the plane u turns about a fixed but arbitrary point (y_1, y_2, y_3, y_4) so that we have

$$\rho \Sigma u_i y_i = \Sigma a_{ij} y_i x_j = 0.$$

From this it appears that the corresponding point x lies on the plane v, where

$$\tau v_j = \Sigma a_{ij} y_i,$$

or

$$\tau v_i = \Sigma a_{ji} y_j. \tag{2}$$

This plane v will coincide with the plane which corresponds to y under (1) if, and only if, there exists a number $\lambda \neq 0$ such that

$$\Sigma a_{ij} y_j = \lambda \Sigma a_{ji} y_j,$$

or

$$\Sigma (a_{ij} - \lambda a_{ji}) y_j = 0 \qquad (i = 1, \cdots, 4). \tag{3}$$

In order that such a point y may arise it is necessary and sufficient that λ be so chosen that the determinant $| A - \lambda A' |$ vanish; i.e., that λ be a root of the equation

$$(4) \qquad D(\lambda) \equiv | A - \lambda A' | = \begin{vmatrix} a_{11} - \lambda a_{11} & \cdots & a_{11} - \lambda a_{11} \\ \cdots\cdots & \cdots\cdots & \cdots\cdots \\ a_{41} - \lambda a_{14} & \cdots & a_{44} - \lambda a_{44} \end{vmatrix} = 0.$$

Similarly, as the point x moves about in a plane v, the plane u corresponding to x will turn about the point y which corresponds to v under (1′) if, and only if, there exists a number $\lambda \neq 0$ such that

$$(5) \qquad \Sigma(A_{ij} - \lambda A_{ji})v_j = 0. \qquad (i = 1, \cdots, 4).$$

That is, λ must be a root of the equation

$$(6) \qquad \bar{D}(\lambda) = | (A^{-1})' - \lambda A^{-1} | = 0,$$

where $(A^{-1})'$ is the transpose of the inverse of A.

The equations (4) and (6) are equivalent. For from the matricial relation

$$(7) \qquad A - \lambda A' = A'[(A^{-1})' - \lambda A^{-1}]A,$$

we have on taking determinants

$$D(\lambda) = | A |^2 \cdot \bar{D}(\lambda).$$

Moreover, it is obvious from (7) that the matrices $A - \lambda A'$ and $(A^{-1})' - \lambda A^{-1}$ are of the same rank, so that there are just as many linearly independent planes v satisfying (5) as there are points y satisfying (3).

Suppose now that y is a point satisfying (3) and that v is the plane corresponding to y under (1); *i.e.*,

$$(3) \qquad \Sigma a_{ij} y_j = \lambda \Sigma a_{ji} y_i ,$$

$$(8) \qquad \Sigma a_{ij} y_j = \rho v_i$$

On substituting ρv_i for the left member of (3), multiplying through by A_{ri} and summing as to i, we get

$$\rho \Sigma A_{ri} v_i = \lambda \Sigma\Sigma A_{ri} a_{ji} y_j = \lambda \mid A \mid y_r .$$

But from (8) we have on multiplying through by A_{ir} and summing as to i,

$$| A | y_r = \rho \Sigma A_{ir} v_i ,$$

whence

$$\Sigma(A_{ri} - \lambda A_{ir})v_i = 0.$$

That is, *if y is a point satisfying* (3), *its corresponding plane v satisfies* (5) *with the same value of* λ. Such a pair (y, v) we call a *double pair* of the correlation *arising from the root* λ.[1]

2. *Projectively Equivalent Correlations.* Suppose now that the points and planes of space be referred to a different tetrahedron of reference. The coördinates x and the coördinates x' of the same point referred to the two different frames are connected by relations of the type

$$\rho x_i = \Sigma p_{ij} x_j' \qquad |P| = |p_{ij}| \neq 0. \tag{9}$$

Moreover, the relations between the coördinates u and the coördinates u' of a plane referred to the two frames are

$$t'u_i = \Sigma P_{ij} u_j', \tag{9'}$$

where P_{ij} is the cofactor of p_{ij} in the determinant $|P|$. On eliminating the u's and x's from (1), (9) and (9'), we obtain

$$\rho' u_i' = \Sigma q_{ij} x_j', \tag{10}$$

where the matrix Q is equal to $P'AP$.

The equations (10) may be thought of either as defining the correlation (1), the points and planes of space now being referred to a new frame of reference, or as defining a correlation projectively equivalent to (1), the frame of reference being the same.

Conversely, a correlation (1) of matrix A and a correlation (10) of matrix Q will be projectively equivalent if, and only if, there exists a non-singular matrix P such that $Q = P'AP$; i.e., if and only if the matrices A and Q are *congruent*.[2]

3. *The Work of Kronecker and Segre.* Kronecker[3] has shown that two non-singular square matrices A and Q of the same order will be

[1] It is clear that the equations (2) also determine a correlation which has as its matrix the transpose matrix A' of A, and which will therefore be identical with (1) if, and only if, A is symmetric. We call (2) the correlation *induced* by (1). By reference to (3) and (5) it is easy to see that a double pair (y, v) of (1) will be a double pair of (2) also. Moreover, by the symmetry of the formulas and equations with respect to A and A', it will follow that the two quadrics, shown subsequently to be associated with (1), will coincide with those associated with (2), and that the properties of the two correlations are identical. We shall therefore confine our attention to (1) only.

[2] Muth, *Theorie und Anwendung der Elementartheiler*, Leipzig, 1899, p. 142.

[3] Muth, *loc. cit.*, p. 143; cf. also Kronecker, *Über die congruenten Transformationen der bilinearen Formen*, Werke, Vol. I, pp. 424–483.

congruent if, and only if, there exist two non-singular matrices R and S such that

$$Q - \lambda Q' = R(A - \lambda A')S,$$

and hence, if and only if the two λ-matrices $Q - \lambda Q'$, $A - \lambda A'$ have the same elementary divisors. The problem of determining whether or not two correlations are projectively equivalent is reduced therefore to a problem in the theory of elementary divisors. By means of this theory it is shown that there are 15 distinct types of non-singular correlations in space, while among correlations of the same type there may be some which are projectively non-equivalent. The normal forms of these types are listed by Muth.[4]

The algebraic work of Kronecker has been interpreted geometrically by Segre,[5] who gives the geometric properties, both from the point of view of line geometry and from the point of view of the ordinary geometry of point and plane.

4. *Purpose of this paper.* It is the purpose of this paper to give a projective classification of non-singular correlations in space without making any use of the theory of elementary divisors. Such classifications for correlations in the plane are well known, such for example, as that given by Woods,[6] and the one given quite recently by the author and C. A. Denson.[7] The method employed here is an extension to three dimensions of that employed in the latter paper. The classification is made on the basis of certain invariants, the roots of the equation $D(\lambda) = | A - \lambda A' | = 0$, and the rank of the associated matrix $A - \lambda A'$, and on the mutual relationship between two associated quadrics. We do not attempt to develop criteria for distinguishing between two non-equivalent correlations of the same type, although it will follow from Kronecker's theory that the distinction can be made very readily through the roots of $D(\lambda) = 0$. Our purpose is merely to establish certain very simple tests whereby it can be determined to which of the 15 types a given correlation belongs, and in addition

[4] Muth, *loc. cit.*, p. 150.

[5] Segre, *Ricerche sulle omografie e sulle correlazioni in generale*, Mem. della Ac. delle Scienze di Torino, Ser. 2, Vol. 37 (1886), pp. 395–435.

[6] Woods, Higher Geometry, Boston (1922), pp. 88–94.

[7] *The Classification of Correlations in the Plane*, American Mathematical Monthly, Vol. 44 (1937), pp. 566–573.

to derive in somewhat greater detail the geometric properties of each type which for the most part are merely listed by Segre.

5. *The Quadrics S and Σ; Points and Planes of Double Pairs.* Much of the preliminary discussion necessary for a classification of correlations in space can be taken over almost bodily from the corresponding discussion for the plane. Indeed, if in the aforementioned paper,[8] the word *plane* be substituted for *line*, *quadric* be substituted for *conic*, and the summation range be extended from 1 to 4 instead of from 1 to 3, it will be easy to see that the proofs remain valid in the extended domain. We shall therefore merely state the following theorems:

THEOREM I. *A point x and the plane u corresponding to it under* (1) *will be in united position if, and only if, x is a point of a quadric S of matrix* $\frac{1}{2}(A + A')$, *and u is a plane of a quadric* Σ *of matrix* $\frac{1}{2}[A^{-1} + (A^{-1})']$. *The quadrics S and* Σ *are of the same rank.*

THEOREM II. *A point y and a plane v of a double pair* (y, v) *arising from a root* $\lambda \neq 1$ *of* $D(\lambda) = 0$ *are always in united position; y is therefore a point of S and v is a plane of* Σ.

THEOREM III. *If* -1 *is a root of the equation* $D(\lambda) = 0$, *the quadric* $S(\Sigma)$ *is singular and the point y (plane v) of the double pair* (y, v) *arising from the root* -1 *is a singular point (plane) of the surface.*

THEOREM IV. *If y and v are point and plane of a double pair* (y, v) *arising from a root* $\lambda \neq -1$ *of* $D(\lambda) = 0$, *then y and v are pole and polar as to the quadrics S and* Σ. *In particular, if y is a point of S and therefore v a plane of* Σ, *then v is a common tangent plane to S and* Σ *at the point y.*

THEOREM V. *If y and v are point and plane of a double pair* (y, v) *arising from a root* $\lambda \neq \pm 1$ *of* $D(\lambda) = 0$, *then v is a common tangent plane to S and* Σ *at y.*

Just as in the case of correlations in the plane, so also here it is evident at once by reference to equation (17) below that the equation $D(\lambda) = 0$ is a reciprocal equation. However, we append here a proof that is valid for a non-singular matrix A of any finite order n.

THEOREM VI. *If A is a non-singular matrix of order n, the equation* $D(\lambda) = |A - \lambda A'| = 0$ *is a reciprocal equation.*

[8] American Mathematical Monthly, Vol. 44, *loc. cit.*, pp. 566–573.

Since by hypothesis A is non-singular, the equation $D(\lambda) = 0$ cannot have the root $\lambda = 0$. Transposing the determinant about its main diagonal, we have

$$D(\lambda) = |A' - \lambda A| = (-\lambda)^n \left| -\frac{1}{\lambda} A' + A \right| = (-\lambda)^n D\left(\frac{1}{\lambda}\right).$$

The theorem is therefore proved.

We now establish two theorems that were not proved in the previous paper.

THEOREM VII. *If (y, v) and (y', v') are two double pairs arising from the roots λ and λ', respectively, of $D(\lambda) = 0$, and if $\lambda' \neq \frac{1}{\lambda}$, then y lies on v' and y' lies on v.*

From (3) we have

$$\Sigma a_{ij} y_j = \lambda \Sigma a_{ji} y_j ,$$

$$\Sigma a_{ij} y'_j = \lambda' \Sigma a_{ji} y'_j .$$

Multiply the first of these equations through by y'_i and sum as to i; similarly, multiply the second through by y_i and sum as to i. We then have

$$\Sigma a_{ij} y'_i y_j = \lambda \Sigma a_{ji} y'_i y_j = \lambda \Sigma a_{ij} y_i y'_j ;$$

$$\Sigma a_{ij} y_i y'_j = \lambda' \Sigma a_{ji} y_i y'_j = \lambda' \Sigma a_{ij} y'_i y_j .$$

Combining these last two equations, we have

$$\Sigma a_{ij} y'_i y_j = \lambda\lambda' \Sigma a_{ij} y'_i y_j ,$$

whence, since $\lambda\lambda' \neq 1$,

$$\Sigma a_{ij} y'_i y_j = 0.$$

By reference to (1) it is seen that this is precisely the condition that y' lie on v. Similarly, y lies on v'.

THEOREM VIII. *If ρ is a root $\neq \pm 1$ of $D(\lambda) = 0$ and if the matrix $A - \rho A'$ is of rank 3, the plane v of the double pair (y, v) arising from the root ρ will pass through the point y' of the double pair (y', v') arising from the root $\frac{1}{\rho}$ if, and only if, ρ is a multiple root of $D(\lambda) = 0$.*

The matrices $A - \rho A'$ and $A - \frac{1}{\rho} A'$ are obviously of the same rank

so that there is a single point y' and a single plane v' arising from the root $\frac{1}{\rho}$. Let us now choose the point y as the vertex (1,0,0,0) of our tetrahedron of reference. Since by hypothesis $\rho \neq \pm 1$, by Theorem II v passes through y. We may then choose v as the plane $x_4 = 0$. By using equations (1) and (3) it is then easy to verify that the matrix A of the correlation will be of the form:

$$A = \begin{pmatrix} 0 & 0 & 0 & a_{14} \\ 0 & a_{22} & a_{23} & a_{24} \\ 0 & a_{32} & a_{33} & a_{34} \\ \rho a_{14} & a_{42} & a_{43} & a_{44} \end{pmatrix} \qquad (a_{14} \neq 0).$$

If for this matrix we form the determinant $| A - \lambda A' |$, we find that

$$D(\lambda) = -a_{14}^2(\rho - \lambda)(1 - \rho\lambda)\, F(\lambda),$$

where

$$F(\lambda) = \begin{vmatrix} a_{22}(1 - \lambda) & a_{23} - \lambda a_{32} \\ a_{32} - \lambda a_{23} & a_{33}(1 - \lambda) \end{vmatrix}.$$

The coördinates (y_1', y_2', y_3', y_4') of the point y' arising from the root $\frac{1}{\rho}$ are proportional to the cofactors of the elements in the first row of $A - \frac{1}{\rho} A'$. We may therefore take as y_4':

$$y_4' = -a_{14}\left(\rho - \frac{1}{\rho}\right) F\left(\frac{1}{\rho}\right).$$

Since $\rho \neq \pm 1$, this point will lie on the plane $x_4 = 0$ if, and only if, $F\left(\frac{1}{\rho}\right) = 0$; *i.e.*, $\frac{1}{\rho}$, and hence ρ, is a multiple root of $D(\lambda) = 0$.

6. *Canonical Form for the Matrix of a Non-singular Correlation.* Since the matrix $B = \frac{1}{2}(A + A')$ of the quadric surface S is symmetric, there exists a non-singular matrix P such that $P'BP = N$, where N consists of zeros except in the diagonal. The elements in the diagonal of N are the coefficients a, b, c, d in the canonical equation of S:

$$ax_1^2 + bx_2^2 + cx_3^2 + dx_4^2 = 0. \tag{11}$$

Geometrically, this means that we have chosen as tetrahedron of reference a self-polar tetrahedron with respect to S.[9] Since $C = \frac{1}{2}(A - A')$ is skew symmetric, so also is $P'CP$. Hence $P'AP = P'(B + C)P$ is of the form:

$$P'AP = \begin{pmatrix} a & h & -g & l \\ -h & b & f & m \\ g & -f & c & n \\ -l & -m & -n & d \end{pmatrix}, \tag{12}$$

where

$$\Delta = abcd + (abn^2 + acm^2 + bcl^2 + adf^2 + bdg^2 + cdh^2) + (fl + gm + hn)^2 \neq 0. \tag{13}$$

Hence, (12) is a canonical form to which the matrix of any non-singular space correlation can be reduced. With A in this form, the matrix $A - \lambda A'$ assumes the simple form:

$$A - \lambda A' = \begin{pmatrix} a(1-\lambda) & h(1+\lambda) & -g(1+\lambda) & l(1+\lambda) \\ -h(1+\lambda) & b(1-\lambda) & f(1+\lambda) & m(1+\lambda) \\ g(1+\lambda) & -f(1+\lambda) & c(1-\lambda) & n(1+\lambda) \\ -l(1+\lambda) & -m(1+\lambda) & -n(1+\lambda) & d(1-\lambda) \end{pmatrix}. \tag{14}$$

If now for brevity we denote by φ and K the expressions

$$\varphi = abn^2 + acm^2 + bcl^2 + adf^2 + bdg^2 + cdh^2, \tag{15}$$

$$K = fl + gm + hn, \tag{16}$$

we have

$$\Delta = abcd + \varphi + K^2 \tag{13'}$$

and

$$D(\lambda) = abcd(1 - \lambda)^4 + \varphi(1 - \lambda)^2(1 + \lambda)^2 + K^2(1 + \lambda)^4. \tag{17}$$

[9] Bôcher, *Introduction to Higher Algebra*, New York, (1907), pp. 124-125.

It can now be verified at the expense of some computation that with A in the form (12), the matrix $A^{-1} + (A^{-1})'$ of the quadric Σ in plane coördinates is

$$\Sigma: \begin{pmatrix} bcd + bn^2 + cm^2 + df^2 & dfg - clm & dfh - bln & chm - bgn \\ dfg - clm & acd + an^2 + cl^2 + dg^2 & dgh - amn & afn - chl \\ dfh - bln & dgh - amn & abd + am^2 + bl^2 + dh^2 & bgl - afm \\ chm - bgn & afn - chl & bgl - afm & abc + af^2 + bg^2 + ch^2 \end{pmatrix} \tag{18}$$

7. *Conditions that the Quadrics S and Σ Coincide.* Let us suppose that $abcd \neq 0$ so that S and Σ are non-singular quadrics. The equation of S in plane coördinates is then

$$\hat{S}: \qquad bcdu_1^2 + acdu_2^2 + abdu_3^2 + abcu_4^2 = 0.$$

It is clear then that S and Σ will coincide if, and only if,

$$\begin{aligned} dfg &= clm \qquad dgh = amn \\ dfh &= bln \qquad afn = chl \\ chm &= bgn \qquad bgl = afm, \end{aligned} \tag{19}$$

and in addition there exists a number $\tau \neq 0$ such that

$$\begin{aligned} bcd(1 - \tau) + bn^2 + cm^2 + df^2 &= 0, \\ acd(1 - \tau) + an^2 + cl^2 + dg^2 &= 0, \\ abd(1 - \tau) + am^2 + bl^2 + dh^2 &= 0, \\ abc(1 - \tau) + af^2 + bg^2 + ch^2 &= 0. \end{aligned} \tag{20}$$

We may state these results in the form of a theorem.

THEOREM IX. *If $abcd \neq 0$, the quadrics S and Σ will coincide if, and only if, the conditions* (19) *hold, and in addition there exists a number $\tau \neq 0$ such that* (20) *holds.*

8. *Enumeration of Cases.* From (17) it is clear that $\lambda = 1$ is a root of $D(\lambda) = 0$ if, and only if, $K = 0$, in which case 1 is at least a double root. Similarly, -1 is a root if, and only if, $abcd = 0$ in which case

this root is at least a double root. On reflection it will be clear that the following cases, and these only, can arise:

Case I. $D(\lambda) = 0$ has the roots 1,1,1,1. Then $\varphi = 0$, $K = 0$, $abcd \neq 0$.

Case II. $D(\lambda) = 0$ has the roots $1,1,-1,-1$. Then $K = 0$, $\varphi \neq 0$, $abcd = 0$, but $(a,b,c,d) \neq (0,0,0,0)$.

Case III. $D(\lambda) = 0$ has the roots $-1, -1, -1, -1$. Then $abcd = 0$, $\varphi = 0$, $K \neq 0$.

Case IV. $D(\lambda) = 0$ has the roots $1, 1, \lambda, \frac{1}{\lambda}$; $(\lambda \neq \pm 1)$. Here $abcd \neq 0$, $\varphi \neq 0$, $K = 0$. If we write $\frac{1-\lambda}{1+\lambda} = \mu$, $(0 \neq \mu \neq \pm 1)$ then μ is a root of the quadratic

$$abcd\mu^2 + \varphi = 0. \tag{21}$$

Note that replacing μ by $-\mu$ replaces λ by $\frac{1}{\lambda}$.

Case V. $D(\lambda) = 0$ has the roots $-1, -1, \lambda, \frac{1}{\lambda}$; $(\lambda \neq \pm 1)$. Here $\varphi \neq 0$, $K \neq 0$, $abcd = 0$, but $(a,b,c,d) \neq (0,0,0,0)$. Also $\mu = \frac{1-\lambda}{1+\lambda}$ is a root of

$$\varphi\mu^2 + K^2 = 0. \tag{22}$$

Case VI. $D(\lambda) = 0$ has the roots $\lambda, \frac{1}{\lambda}, \lambda, \frac{1}{\lambda}$. Here $abcd \neq 0$, $\varphi \neq 0$, $K \neq 0$, and the equation

$$abcd\mu^4 + \varphi\mu^2 + K^2 = 0 \tag{23}$$

considered as a quadratic in μ^2 has a double root; i.e.,

$$\varphi^2 - 4abcdK^2 = 0. \tag{24}$$

Case VII. $D(\lambda) = 0$ has the roots $\lambda_1, \frac{1}{\lambda_1}, \lambda_2, \frac{1}{\lambda_2}$. Here we have the same conditions as in Case VI, except that the quadratic (23) in μ^2 has distinct roots.

These seven cases subdivide further according to the rank of the associated matrix $A - \lambda A'$ and to the mutual relationship of the quadrics S and Σ. In fact, as we shall see, there are 15 distinct types of correlations in space. In order to facilitate comparison of the cases

as arrived at here with the canonical forms as listed by Muth, we shall in each case refer to the number of the corresponding form given by Muth, *loc. cit.*, p. 150.

9. Case I. $D(\lambda) = 0$ has the roots 1,1,1,1. Since $abcd \neq 0$, the quadrics S and Σ are non-singular. All points of double pairs are obtained by solving the equations (3) with $\lambda = 1$. The matrix $A - A'$ of this system is skew-symmetric, its determinant being $16K^2 = 0$. Hence the rank of the matrix is 0 or 2.[10]

Case I-1. If the matrix $A - A'$ is of rank 0, then f, g, h, l, m, n are all zero. The matrix A of the correlation is therefore symmetric. Moreover, the conditions (19) and (20) are obviously satisfied, the latter with $\tau = 1$, so that the quadrics S and Σ coincide. Every point y in space is a point of a double pair (y, v), the plane v corresponding to y being the polar plane of y as to S. This is the so-called *polarity*.[11] It is Muth's case 11.

Case I-2. Suppose next that the matrix $A - A'$ is of rank 2. Then since f, g, h, l, m, n are not all zero, it is a matter of notation to suppose that $h \neq 0$. There is an entire line L of points y of double pairs (y, v), the equations of which may be taken as

$$(25)\quad L: \qquad \begin{aligned} hx_2 - gx_3 + lx_4 &= 0 \\ -hx_1 + fx_3 + mx_4 &= 0. \end{aligned}$$

In terms of the parameters ξ, η the coördinates of a typical point y on L may be written:

$$(26)\quad y: \qquad (f\xi + m\eta,\ g\xi - l\eta,\ h\xi,\ h\eta).$$

By Theorem IV the plane v corresponding to y under the correlation is the polar plane of y as to S; *i.e.*,

$$(27)\quad v: \qquad (af\xi + am\eta,\ bg\xi - bl\eta,\ ch\xi,\ dh\eta).$$

As y runs along L, v turns about the line M

$$(28)\quad M: \qquad \begin{aligned} afx_1 + bgx_2 + chx_3 &= 0 \\ amx_1 - blx_2 + dhx_4 &= 0, \end{aligned}$$

which is the conjugate line of L as to S.

[10] Bôcher, *loc. cit.*, Ex. 4, p. 59.
[11] Woods, *loc. cit.*, p. 247.

The lines L and M have at least one point in common, the coördinates of which may be taken as any one of the following sets which does not consist entirely of zeros:

$$T: \begin{matrix} (bn^2+cm^2+df^2, & dfg-clm, & dfh-bln, & chm-bgn) \\ (dfg-clm, & an^2+cl^2+dg^2, & dgh-amn, & afn-chl) \\ (dfh-bln, & dgh-amn, & am^2+bl^2+dh^2, & bgl-afm) \\ (chm-bgn, & afn-chl, & bgl-afm, & af^2+bg^2+ch^2) \end{matrix}$$

If all of the above sets vanish, L coincides with M. Moreover, the conditions (19) and (20) are evidently satisfied, the latter with $\tau = 1$, so that by Theorem IX the quadrics S and Σ coincide. Conversely, if the quadrics coincide the lines L and M are identical.

Both of the foregoing situations actually arise and we have a separation of cases.

Case I-21. Here the quadrics S and Σ coincide. There is a line L (25) of points of double pairs which is a generator of S and as the point y moves along L, its corresponding plane v turns about L. This is Muth's Case 14.

Case I-22. Here the quadrics S and Σ do not coincide. L and M intersect in a unique point T which lies on S, and the tangent plane π to S at T is the plane of L and M. Hence, by Theorem IV, S and Σ are tangent to each other at T. But further from (18) and from the plane equation of S it can be verified that

$$\Sigma - \hat{S} = k(\Sigma\alpha_i u_i)^2,$$

where the α's are the coördinates of T.

If in §6, instead of so choosing the tetrahedron of reference that the equation of S is in canonical form, we should choose the tetrahedron so that the equation of Σ is in canonical form, the rôles of S and Σ would be interchanged. We can conclude then that if $\hat{\Sigma} = 0$ is the point equation of Σ, then

$$\hat{\Sigma} - S = k'(\Sigma\beta_i x_i)^2,$$

where the β's are the coördinates of the tangent plane π to S at T. Hence, the only points common to S and Σ are those in which π intersects S; i.e., the two generators through T. It can be shown that the two quadrics are tangent along these two generators and that the lines L and M separate these two generators harmonically. This is Muth's Case 13.

It will be noted in the work that follows that in this one case only, *viz.*, in distinguishing between Cases I-21 and I-22, do we find it necessary to invoke the relationship between the quadrics S and Σ. In all other cases the types of correlations are distinguished from one another by the roots of the equation $D(\lambda) = 0$ and the rank of the associated matrix $A - \lambda A'$.

10. Case II. $D(\lambda) = 0$ has the roots 1, 1, -1, -1. Here $K = 0$, $abcd = 0$, $\varphi \neq 0$, and not more than two of a, b, c, d can be zero since $\varphi \neq 0$. There is a separation of cases according to the number of coefficients in (11) that vanish, i.e., according as the rank of S is 3 or 2.

Case II-1. $a = 0$, $bcd \neq 0$, $\varphi = bcl^2 + bdg^2 + cdh^2 \neq 0$.

Case II-2. $a = b = 0$, $cd \neq 0$, $\varphi = cdh^2 \neq 0$.

Case II-1. The quadrics S and Σ are of rank 3. S is a proper cone

$$bx_2^2 + cx_3^2 + dx_4^2 = 0, \tag{29}$$

with vertex V: (1, 0, 0, 0). The matrix of Σ in plane coördinates is (18) with $a = 0$. Σ is a pencil of planes of the second order and the singular plane is v: $(0, h, -g, l)$, the plane corresponding to V under the correlation. Evidently v passes through V. But it is not a proper tangent plane to S. To show this, we note that h, g, l cannot all be zero since $\varphi \neq 0$. If then we assume that $h \neq 0$, the line joining the two distinct points $(0, g, h, 0)$, $(0, l, 0, -h)$ on v will be tangent to S if, and only if, the quadratic

$$b(\xi g + l)^2 + ch^2\xi^2 + dh^2 = 0 \tag{30}$$

in ξ has equal roots. But the discriminant is

$$(bg^2 + ch^2)(bl^2 + dh^2) - b^2g^2l^2 = h^2\varphi \neq 0. \tag{31}$$

We seek now for points y of double pairs. Corresponding to the root 1 we find an entire line L of such points whose equations are given in (25). The planes corresponding to points on L all pass through the line M whose equations are given by (28) with $a = 0$,

$$M: \quad bgx_2 + chx_3 = 0, \quad -blx_2 + dhx_4 = 0. \tag{28'}$$

M passes through V but does not meet L. It is evident that L lies in the singular plane v, and since v is not tangent to S, L is neither a tangent nor a ruling of S. There are, therefore, just two points, P and Q, which lie on their corresponding planes, p and q. These two

planes are tangent to S at P and Q, respectively, and it is easy to verify that they intersect in M.

Consider now the root -1. The matrix of the system (3) is then (14) with $a = 0$ and $\lambda = -1$. This is evidently of rank 3, so that corresponding to the root -1 there is a single point (1, 0, 0, 0) of a double pair. This point is precisely the vertex V of the cone S. This is Muth's case 10.

Case II-2. Here $a = b = 0$, $K = 0$, $cdh^2 \neq 0$. The quadrics S and Σ are of rank 2 so that S consists of two planes and Σ consists of two points. If in the matrix (12) we put $a = b = 0$, $c = \alpha^2$, $d = -\beta^2$, the equation of S becomes

$$S: \quad \alpha^2 x_3^2 - \beta^2 x_4^2 = 0.$$

Hence, S degenerates into the two planes

$$\begin{aligned} \pi_1&: \alpha x_3 - \beta x_4 = 0, \\ \pi_2&: \alpha x_3 + \beta x_4 = 0, \end{aligned} \tag{32}$$

which intersect in the line M: $x_3 = 0$, $x_4 = 0$. By referring to (18) it will be seen that the equation of Σ can be written

$$\Sigma: \quad \alpha^2(mu_1 - lu_2 + hu_4)^2 - \beta^2(fu_1 + gu_2 + hu_3)^2 = 0,$$

so that the coördinates of the two points P_1 and P_2 of Σ are

$$\begin{aligned} P_1&: \quad (m\alpha + f\beta, -l\alpha + g\beta, \quad h\beta, h\alpha) \\ P_2&: \quad (m\alpha - f\beta, -l\alpha - g\beta, -h\beta, h\alpha). \end{aligned} \tag{33}$$

Evidently P_1 lies on π_1 and P_2 lies on π_2. Moreover, π_1 and π_2 correspond to P_1 and P_2, respectively, under the correlation.

Let us now seek the points and planes of double pairs. Corresponding to the root $\lambda = 1$, we get as before a line L of points whose equations are given by (25). It is evident that L passes through P_1 and P_2. As the point P whose coördinates are given by (26) moves along L, its corresponding plane

$$\alpha^2 \xi x_3 - \beta^2 \eta x_4 = 0$$

turns about the line M and intersects L in the point T:

$$(f\beta^2 \eta + m\alpha^2 \xi, g\beta^2 \eta - l\alpha^2 \xi, \beta^2 h\eta, \alpha^2 h\xi).$$

It is easy to verify that P and T separate P_1 and P_2 harmonically.

Since the matrix $A + A'$ is the matrix (14) with $a = b = 0$, $\lambda = -1$, its rank is 2, so that corresponding to the root -1 there is a line of

points of double pairs, *viz.*, the line M. As a point Q moves along M, the plane corresponding to Q passes through Q and turns about L. This is Muth's case 12.

11. Case III. $D(\lambda) = 0$ has the roots $-1, -1, -1, -1$. Here $abcd = 0, \varphi = 0, K \neq 0$. There are four subcases.

Case III-1. $a = 0, bcd \neq 0$.

Case III-2. $a = b = 0, cd \neq 0; \varphi = cdh^2 = 0, h = 0$.

Case III-3. $a = b = c = 0, d \neq 0$.

Case III-4. $a = b = c = d = 0$.

Case III-1. The quadric S is a proper cone (29) with vertex V: (1,0,0,0). Σ is a pencil of planes of the second order, the singular plane being, as in Case II-1, v: $(0, h, -g, l)$.

Since $\varphi = 0$, the discriminant (31) of the quadratic (30) is zero, so that v is a proper tangent plane to S. If we denote by Q the point

$$Q\text{: } (0, cl^2 + dg^2, dgh, -chl),$$

it is easy to see that v is tangent to S along the line VQ, and, as a point P moves along VQ, the plane π corresponding to P turns about VQ.

The only point of a double pair is the vertex V of S, the plane corresponding to V being the singular plane v of Σ. This is Muth's case 8.

Case III-2. $a = b = 0, cd \neq 0, K \neq 0$. If, as in Case II-2, we put $c = \alpha^2, d = -\beta^2$, we have as the planes of S the two planes π_1 and π_2 in (32), while Σ consists of the two points P_1 and P_2 whose coördinates are obtained by putting $h = 0$ in (33). The planes π_1 and π_2 correspond to P_1 and P_2, respectively, under the correlation, and the line of intersection of the two planes is the line P_1P_2. This line is therefore a line of points of double pairs.

As a point Q moves about in the plane π_1, its corresponding plane passes through P_1 and Q; *i.e.*, the plane turns about the line P_1Q as an instantaneous axis. This is Muth's case 7.

Case III-3. $a = b = c = 0, d \neq 0, K \neq 0$. The quadric S consists of the plane π: $x_4 = 0$, repeated. The quadric Σ consists of the point P: $(f, g, h, 0)$, repeated. P lies on π and corresponds to it under the correlation. Each point of π is a point of a double pair. The plane corresponding to a point Q of π passes through Q and P, *i.e.*, as Q moves about in the plane π, the plane corresponding to Q turns about PQ as an instantaneous axis. This is Muth's case 9.

Case III-4. $a = b = c = d = 0, K \neq 0$. The quadrics S and Σ are of rank zero. We may then think of S as consisting of all points in space and of Σ as all planes in space. Every point P in space is a

point of a double pair (P, π), where P lies on π. This is the *Null System* of Möbius,[12] and is Muth's case 15.

12. *Rank of the Matrix* $A - \lambda A'$ *for* $\lambda \neq -1$. Before proceeding to a discussion of cases IV, V, VI and VII we shall find it desirable to establish a lemma. It is obvious that for $\lambda \neq -1$, the matrix $A - \lambda A'$ in (14) can be written

$$A - \lambda A' = (1 + \lambda)\begin{pmatrix} a\mu & h & -g & l \\ -h & b\mu & f & m \\ g & -f & c\mu & n \\ -l & -m & -n & d\mu \end{pmatrix}, \tag{14'}$$

where $\mu = \dfrac{1 - \lambda}{1 + \lambda}$. If then λ is a root $\neq -1$ of $D(\lambda) = 0$, we write $D(\lambda) = (1 + \lambda)^4 F(\mu)$, where

$$F(\mu) = abcd\mu^4 + \varphi\mu^2 + K^2. \tag{17'}$$

We now prove the lemma:

Lemma. If $\lambda \neq -1$ is a root of $D(\lambda) = 0$, the matrix $A - \lambda A'$ on the right in (14') is of rank less than 3 only if μ is a multiple root of (17').

For the third order principal minors of $A - \lambda A'$ are, save for the factor $(1 + \lambda)^3$:

$$\mu(bcd\mu^2 + bn^2 + cm^2 + df^2),$$
$$\mu(acd\mu^2 + an^2 + cl^2 + dg^2),$$
$$\mu(abd\mu^2 + am^2 + bl^2 + dn^2),$$
$$\mu(abc\mu^2 + af^2 + bg^2 + ch^2).$$

If all these principal minors vanish, we have, on multiplying through by a, b, c and d, respectively, and adding,

$$4abcd\mu^3 + 2\varphi\mu = 0;$$

that is, $F'(\mu) = 0$, so that μ is a multiple root of (17').

13. Case IV. $D(\lambda) = 0$ has the roots 1, 1, λ, $\dfrac{1}{\lambda}$; $(\lambda \neq \pm 1)$. Here $abcd \neq 0$, $\varphi \neq 0$, $K = 0$. If $\mu = \dfrac{1 - \lambda}{1 + \lambda}$, then μ is a root of

$$abcd\mu^2 + \varphi = 0.$$

[12] Woods, *loc. cit.*, p. 248.

The quadrics S and Σ are non-singular. Since $\varphi \neq 0$, we cannot have f, g, h, l, m, n all zero. Hence the matrix $A - A'$ is of rank 2, so that corresponding to the root 1 there is a line L of points of double pairs, whose equations for $h \neq 0$ are given by (25). As a point moves along L, its corresponding plane turns about a line M (28) which is conjugate to L with respect to S. L does not intersect M, neither is it tangent to S, since the discriminant (31) of the quadratic (30) is $h^2\varphi \neq 0$. Hence, L cuts S in two distinct points, T_1 and T_2. The planes corresponding to T_1 and T_2 are by Theorem IV common tangent planes to S and Σ at T_1 and T_2, respectively, and these planes intersect in M.

Consider now the roots λ and $\frac{1}{\lambda}$. By the lemma of the preceding section each of the matrices $A - \lambda A'$ and $A - \frac{1}{\lambda}A'$ is of rank 3, so that corresponding to each of the roots there is a single point of a double pair. By theorems II and IV, these points R_1 and R_2 lie on S and Σ, and the planes corresponding to them are common tangent planes to the two quadrics at R_1 and R_2, respectively. By Theorem VII these two planes intersect in L. Also, by the same theorem, the tangent planes to S at T_1 and T_2 pass through both R_1 and R_2, so that the latter two points are the points of intersection of M with S (and Σ). The two quadrics therefore intersect along the four generators which form the sides of the skew quadrilateral $R_1T_1R_2T_2$, and are tangent at each of the vertices of the quadrilateral. This is Muth's case 6.

14. Case V. $D(\lambda) = 0$ has the roots $-1, -1, \lambda, \frac{1}{\lambda}$; $(\lambda \neq \pm 1)$. Here $\varphi \neq 0$, $K \neq 0$, $abcd = 0$, but not more than two of a, b, c, d can be zero since $\varphi \neq 0$. If as above we write $\mu = \frac{1-\lambda}{1+\lambda}$, then μ is a root of the quadratic equation

$$\varphi\mu^2 + K^2 = 0.$$

Two subcases arise: 1. $a = 0$, $bcd \neq 0$;

$$2.\ a = b = 0,\ cd \neq 0.$$

Case V-1. Here S and Σ are of rank 3. Hence, S is a proper cone with vertex V: (1,0,0,0) as in case II-1. Similarly, Σ is a pencil of planes of the second order whose singular plane v: $(0, h, -g, l)$ corre-

sponds to V under the correlation. The plane v passes through the vertex V of S but is not a proper tangent plane to S.

Corresponding to the root -1 there is a single point V of a double pair (V, v). Consider then the roots $\lambda, \frac{1}{\lambda}$. By the lemma of section 12, the matrices $A - \lambda A'$, $A - \frac{1}{\lambda} A'$ are of rank 3, so that corresponding to each root there is a single point of a double pair. Each of these points R_1 and R_2 lies on one of the generators in which the plane v intersects S, and the tangent planes to S at R_1 and R_2 correspond to the latter under the correlation. This is Muth's case 4.

Case V-2. $a = b = 0, \varphi = cdh^2 \neq 0, K \neq 0$. The situation here is quite similar to that in case II-2. S degenerates into two planes π_1 and π_2, while Σ degenerates into two points P_1 and P_2. P_1 lies on π_1 and P_2 lies on π_2. However, instead of a line L of points of double pairs arising from the double root $\lambda = 1$, here, arising from each of the roots $\lambda, \frac{1}{\lambda}$, there is a single point of a double pair. These points are precisely the points P_1 and P_2 of Σ. This is Muth's case 5.

15. Case VI. $D(\lambda) = 0$ has the roots $\rho, \frac{1}{\rho}, \rho, \frac{1}{\rho}$, $(\rho \neq \pm 1)$. Hence $abcd \neq 0, \varphi \neq 0, K \neq 0$, and the quadratic

$$abcd\mu^4 + \varphi\mu^2 + K^2 = 0 \tag{23}$$

in μ^2 has a double root.

The quadrics S and Σ are non-singular. In seeking for the points and planes of double pairs, it is evident that the matrix $A - \lambda A'$ on the right in (14′) can be of rank 1 only if

$$fl + gm = 0, \quad gm + hn = 0, \quad fl + hn = 0.$$

But on adding it would then follow that $2K = 0$, contrary to hypothesis. There is, however, a separation of cases according as the rank of this matrix is 2 or 3.

Case VI-1. The matrices $A - \rho A'$, $A - \frac{1}{\rho} A'$ of rank 2.

It can be shown without any difficulty that the matrix $A - \rho A'$ will be of rank 2 if, and only if, the conditions (19) and (20) hold, the latter with $1 - \tau$ replaced by μ^2, and in addition we have

$$cdh\mu^2 + nK = 0, \quad bdg\mu^2 + mK = 0, \quad bcl\mu^2 + fK = 0,$$
$$adf\mu^2 + lK = 0, \quad acm\mu^2 + gK = 0, \quad abn\mu^2 + hK = 0.$$

Under these conditions the quadrics S and Σ coincide. Corresponding to each of the roots $\rho, \frac{1}{\rho}$, there is a line of points of double pairs. These lines are by Theorem II rulings of S, and moreover they belong to the same regulus. For if they had a point in common we should have a point of a double pair arising from two distinct roots of $D(\lambda) = 0$. This is Muth's case 2.

Case VI-2. The matrices $A - \rho A'$, $A - \frac{1}{\rho} A'$ of rank 3. In this case the quadrics S and Σ do not coincide. Corresponding to each of the roots $\rho, \frac{1}{\rho}$, there is a single point of a double pair. These two points, P_1 and P_2, lie on both S and Σ, and their corresponding planes, π_1 and π_2, are common tangent planes to S and Σ at P_1 and P_2, respectively. By Theorem VIII π_1 passes through P_2 and π_2 passes through P_1. The line P_1P_2 is a common ruling of S and Σ and the quadrics are tangent at each point of the ruling. This is Muth's case 3.

16. Case VII. $D(\lambda) = 0$ has the roots $\rho, \frac{1}{\rho}, \sigma, \frac{1}{\sigma}$; $(\rho \neq \sigma \neq \pm 1)$. Here $abcd \neq 0, \varphi \neq 0, K \neq 0$, while the quadratic (23) in μ^2 does not have a multiple root. The quadrics S and Σ are non-singular.

By the lemma of section 12 each of the matrices $A - \rho A', \cdots, A - \frac{1}{\sigma} A'$ is of rank 3, so that corresponding to each root of $D(\lambda) = 0$ there is a single point of a double pair. Let (P_1, π_1), (P_2, π_2), (P_3, π_3), (P_4, π_4) be the double pairs arising from the roots $\rho, \frac{1}{\rho}, \sigma, \frac{1}{\sigma}$, respectively. Then by Theorem VII, π_1 passes through P_3 and P_4, but by Theorem VIII does not pass through P_2. Moreover, by Theorem V, P_1 lies on both S and Σ and π_1 is the common tangent plane to the two quadrics at P_1. A similar situation exists among the remaining points and planes of the double pairs. The four points P_1, P_2, P_3, P_4 are therefore vertices of a skew quadrilateral whose sides are two generators from each regulus on S. Moreover, the two quadrics intersect along the above four rulings and are tangent to each other at each of the our points P. This is Muth's case 1.

17. *Summary.* Since under a transformation of the type (12) the determinant $D(\lambda) = |A - \lambda A'|$ is an invariant of index 2, evidently

the roots of $D(\lambda)$ are unaltered and the coefficients $abcd$, φ and K^2 are themselves invariants.[13] Let us as in section 6 write

$$B = \tfrac{1}{2}(A + A'), \quad C = \tfrac{1}{2}(A - A'),$$

Then since we can always, without loss of generality, so choose P in (12) that $|P| = 1$, it is clear that we can take

$$abcd = |B|, \quad K^2 = |C|, \tag{34}$$

whence from (13) it will follow that

$$\varphi = |A| - |B| - |C|. \tag{35}$$

Moreover, it is clear that the rank of B is precisely the number of the quantities a, b, c, d which are different from zero. The 15 cases which have been discussed in sections 8–16 can therefore be characterized completely as follows, it being assumed throughout that the correlation is non-singular, *i.e.*, that $|A| \neq 0$.

Case I-1. The matrix A is symmetric; i.e., $C = 0$.

Case I-21. $|B| = |A|$; C of rank 2; and in addition the quadrics S and Σ coincide, i.e., $(A + A')^{-1} = k[A^{-1} + (A^{-1})']$.

Case I-22. The same as in Case I-21, except that here the quadrics do not coincide.

Case II-1. B of rank 3, C of rank 2.

Case II-2. B of rank 2, C of rank 2.

Case III-1. B of rank 3, $|C| = |A|$.

Case III-2. B of rank 2, $|C| = |A|$.

Case III-3. B of rank 1, $|C| = |A|$.

Case III-4. $B = 0$, *i.e.*, A skew-symmetric.

Case IV. $0 \neq |B| \neq |A|$; C of rank 2.

Case V-1. B of rank 3, $|A| \neq |C| \neq 0$.

Case V-2. B of rank 2, $|A| \neq |C| \neq 0$.

Case VI-1. B of rank 4, C of rank 4, $\varphi = |A| - |B| - |C| \neq 0$ $\varphi^2 - 4|B||C| = 0$; *i.e.* the equation $D(\lambda) = 0$ has the roots $\rho, \frac{1}{\rho}, \rho, \frac{1}{\rho}$ $(\rho \neq \pm 1)$, and the matrix $A - \rho A'$ of rank 2.

Case VI-2. The same as in VI-1, except that the matrix $A - \rho A'$ is of rank 3.

Case VII. B of rank 4, C of rank 4, $\varphi \neq 0$, $\varphi^2 - 4|B||C| \neq 0$ i.e., the equation $D(\lambda) = 0$ has the roots $\rho, \frac{1}{\rho}, \sigma, \frac{1}{\sigma}$; $(\rho \neq \sigma \neq \pm 1)$.

[13] Bôcher, *loc. cit.*, p. 166.

18. *Projective Equivalence of Correlations.* Up to this point in this paper, no use has been made of the results arrived at by Kronecker through the theory of elementary divisors. If, however, we refer to the canonical forms of non-singular correlations as listed by Muth, it will be seen that in each of the cases I-1, I-21, I-22, II-1, II-2, III-1, III-2, III-3, III-4 the canonical form contains no parameter, and hence that any two correlations belonging to one of these types are projectively equivalent. On the other hand, in each of the types IV, V-1, V-2, VI-1, VI-2 the canonical form contains a single parameter C_1, and in each case the equation $D(\lambda) = 0$ has the roots C_1 and $\frac{1}{C_1}$. Furthermore, in Case VII, Muth's canonical form contains two parameters C_1 and C_2, while in this case the equation $D(\lambda) = 0$ has precisely the roots $C_1, \frac{1}{C_1}, C_2, \frac{1}{C_2}$. This leads to the following theorem:

THEOREM X. *Two correlations belonging to one of the above* 15 *types are projectively equivalent if, and only if, their equations* $D(\lambda) = 0$ *are equivalent.*

19. *Illustration.* Consider for example the correlation

$$\rho u = A(x),$$

in which

$$A = \begin{pmatrix} 5 & -6 & 5 & -4 \\ 10 & -1 & 5 & -1 \\ -1 & -1 & 0 & 0 \\ 4 & -1 & 2 & -1 \end{pmatrix}, \qquad |A| = 9.$$

We find immediately that

$$B = \begin{pmatrix} 5 & 2 & 2 & 0 \\ 2 & -1 & 2 & -1 \\ 2 & 2 & 0 & 1 \\ 0 & -1 & 1 & -1 \end{pmatrix}, \qquad C = \begin{pmatrix} 0 & -8 & 3 & -4 \\ 8 & 0 & 3 & 0 \\ -3 & -3 & 0 & -1 \\ 4 & 0 & 1 & 0 \end{pmatrix},$$

whence

$$|B| = abcd = 1, \qquad |C| = K^2 = 16.$$

By (35) we find that $\varphi = -8$. Since all three of the quantities $abcd$, K, φ are different from zero, this correlation belongs either to type VI or to type VII. However, we see at once that

$$\varphi^2 - 4abcdK^2 = 0$$

so that the correlation belongs under type VI. The equation $D(\lambda) = 0$ here is

$$(1 - \lambda)^4 - 8(1 - \lambda)^2(1 + \lambda)^2 + 16(1 + \lambda)^4 = 0,$$

the roots of which are -3, -3, $-1/3$, $-1/3$. Moreover, the matrix $A + 3A'$ is found to be of rank 2. This definitely places the correlation under Case VI-1.

It is easy to verify that corresponding to each of the roots of $D(\lambda) = 0$ the line of points of double pairs is a generator of S and that the quadrics S and Σ coincide.

THE UNIVERSITY OF NORTH CAROLINA,
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INFLUENCE OF TEMPERATURE ON CYCLOMORPHOSIS OF DAPHNIA LONGISPINA[1]

By R. E. Coker and H. H. Addlestone

With 7 Text Figures

I. HISTORICAL REVIEW

Cyclomorphosis

Although Sars (1890), Zacharias (1893, 1894), and Lilljeborg (communication quoted by Zacharias, 1893) had noted the seasonal variation of certain Cladocera, it was Wesenberg-Lund (1900) who first made an extensive study of the cyclomorphosis of pelagic Cladocera, Protozoa, and Algae, and attempted to relate the seasonal changes to the physical conditions of the environment. Animals in summer may be so unlike their ancestors of the preceding winter, or their descendants of the following winter, that systematists have confidently placed them in different species or genera (Daphnia and Hyalodaphnia, or, among Protozoa, Trachelius, Dileptus and Amphileptus). The summer form is marked by elongation of the body, prolongations of the head to form "helmets" (fig. 1, *b*, *c*), spines, etc.—a strong development of the sort of structural features that have naturally suggested the designation" flotation processes." Wesenberg-Lund noted that the contrast of summer forms with winter forms was found only in pelagic organisms (and, as it then seemed, only in fresh-water plankton), not in those that live on the bottom or in the littoral. Among Cladocera, by the way, cyclomorphosis is featured by the females, not by the males, which occur only at certain times or under certain conditions.

Chief Theories as to the Significance and Causes of Cyclomorphosis in Cladocera

It is not unnatural that explanations of the seasonal change of form should be sought in the contrasting physical conditions of the environment in winter and summer. Temperature, specific gravity, viscosity,

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gas content, nutrition would suggest themselves as possibly significant variables; the mineral content of the water could be eliminated as virtually unrelated to the season of the year, however much it might differ from lake to lake. Wesenberg-Lund concluded that it was the changing specific gravity of the water that governed this reversible metamorphosis from generation to generation—a series of changes aptly characterized by Woltereck later as *metagenetic* (as contrasted with ontogenetic or phylogenetic modifications).

W. Ostwald (1902) followed almost immediately with his more ambitious "Theory of the Plankton," in which he (1) analyzed the physical conditions of floating; (2) characterized the plankton as, by definition,

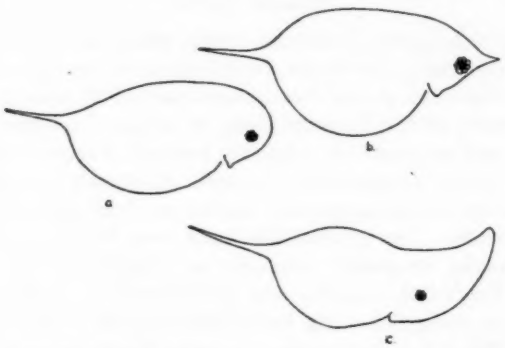

FIG. 1. *a. Daphnia longispina*, from University Lake, Chapel Hill, N. C., winter form (round head; *b.* same, late spring form (helmeted); *c.* Daphnia from Chautauqua Lake, N. Y., summer form.

made up of floating organisms and as possessing characteristic structural features (high water content with consequent translucency of body, oil-droplets, gas vacuoles, gelatinous hulls or bodily extensions in the forms of plates, keels, processes or long plumose setae which were sometimes remarkably developed); and (3) related such features to the continuing and changing conditions of flotation. Marine and fresh-water plankton came within his purview. Like Wesenberg-Lund, he considered the seasonal variations of fresh-water plankton organisms to be adaptations to the seasonal changes in the condition of flotation. Without going into the details of his argument, it is enough to say now that he dismissed specific gravity as the significant variable, since the changes were relatively small and would be parallel for organism and water,

and that he concluded that the changing viscosity of the water with seasonal change of temperature was the determining factor in cyclomorphosis. Viscosity is practically doubled wih a fall of 25° (25°–0°C.). Since we have to refer later to the seeming deficiency of records of precise experimental observation in all the literature that has followed, it should be mentioned here that Ostwald (1904) did conduct experiments with *Hyalodaphnia cristata* at different temperatures, although the conditions of his experiments seem to have been very unfavorable and the results, we should say now, quite inadequate to justify his conclusions.

Rearing *Hyalodaphnia cristata* at different temperatures very roughly controlled, he found that the young of short-helmeted individuals born at high temperatures had longer helmets than their parents and that the offspring of long-helmeted individuals born at low temperatures had shorter helmets than their parents. He was thus comparing young animals that passed through the embryonic stages under laboratory conditions with adults that had developed in the lake. Apparently he did not rear the young to ascertain if the helmets appropriate to the temperature were maintained throughout life at given temperatures, nor did he breed second generations. To an extent the results of his experiments were an indication of a relationship between temperature and form but they seem now to have afforded little support for his unqualified conclusion that seasonal variation in form was a result solely of temperature and that the expression "temporal (or seasonal) variation" should be replaced by "temperature variation" as the more precisely applicable term. It seems not to have been generally noted that Ostwald dealt with the form of the head of the newborn, while Woltereck later seems to have dealt chiefly with the form of the head of the developing young and adults. In nature, according to Wesenberg-Lund (1910), the changes occur chiefly from generation to generation and only to a lesser degree in the ontogeny of the free-swimming individuals. Causes of change may not be identical in the two cases.

Wesenberg-Lund accepted the emendation and the Wesenberg-Lund—Ostwald "Buoyance Theory" won general acceptance for a time; but Woltereck (1909, 1911, 1913, 1920, etc.), most notably, dissented. He found a significant weakness in the theory in that it failed to take proper account either (1) of the relation between the direction of extension of processes and the position of the animal in the water, or (2) of the self-propulsion of the animal. Ostwald had, indeed, considered vertical locomotion of plankton organisms, the energy required for

which was greater with diminished viscosity and consequently greater falling velocity, but he had discounted locomotion in a horizontal direction. In Woltereck's view, helmets, spines, mucros, etc., served like the keel and rudder of a ship as directing and guiding surfaces, whose functions were realized chiefly, if not exclusively, when the animal was in active movement, as it generally was. It was desirable for the animal to remain in a relatively thin layer of water where alone nutritive conditions were satisfactory during the summer period of stratification. The heightened cellular activity leading to the development of protuberances from the body was a more or less direct result of the better nutritive conditions and these protuberances, functioning as keels and rudders, enabled the animal to remain where the nutritive conditions were better.

Changing the viscosity of the medium by the addition of quince jelly had no effect.

Woltereck also introduced the "time factor" (Zeitfactor), measured by the generation number. He has held to the Weismannian idea of a definite reproductive cycle (ephippial egg—so many generations of parthenogenetic females—ephippial egg) now largely, if perhaps not completely, discredited by the work of Grosvenor and Smith (1913), Banta (1914, 1923, etc.), Berg (1932, 1934) and others, who relate the mode of reproduction to environmental conditions. The idea of the reproductive cycle implies that, after the ephippial or resting egg (a sexually fertilized egg), only so many generations (the number varying with the race) of parthenogenetic generations are possible before internal conditions require the production of ephippial eggs. The condition of sexuality, very weak in the exephippial generation, increases from parthenogenetic generation to parthenogenetic generation until it becomes commanding in respect to mode of reproduction.[2] The place of a particular animal in the cycle according to Woltereck was fixed by the number of generations from the ephippial egg—and its capacity to re-

[2] Another version of the reproductive cycle seems to be embodied in the "Depression" idea of Wagler (1923)—according to which there follows a diminution of vitality from generation to generation and from brood to brood—with an increasing tendency to production of males and ephippial females. This conception of a natural depression occurring automatically from internal causes may be contrasted with the view of Berg (1934) that "Depression" artificially produced by the accumulation of waste products or other causes leads to the incidence of sexual reproduction. The two views as to "Depression" really offer diametrically opposite explanations of the control of modes of reproduction, with evidence apparently favoring Berg's view.

act to the more abundant nutrition by change of form was determined in part by this number (fig. 2). The sixth generation with rich nour-

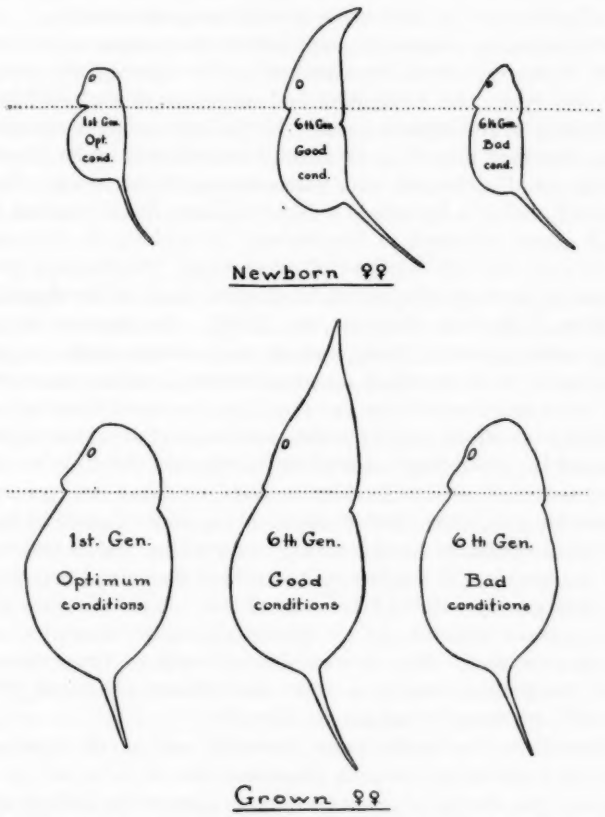

FIG. 2. *Daphnia cucullata.* Illustrating reported influence of conditions of nutrition and generation number on development of the helmet; adapted from Woltereck.

ishment would reproduce a high helmet (at low or high temperatures) but the first or second under like conditions would not.

It is quite impossible within narrow limits of space to review the prolonged discussion in literature where observation, experiment,

theory, argument, and speculation seem sometimes to be almost inextricably mixed. Nevertheless, in order measurably to clear the atmosphere and set the necessary background for our own experimental work, a further brief, if inadequate, review seems necessary.

Wesenberg-Lund's extensive and careful observations over a period of years in many waters, his synthesis of the observations made by himself and others, his recognition and statement of the problem were contributions of the highest value. He did not conduct experiments and has expressed himself as doubtful if experiments under laboratory conditions could be of much value with reference to his theory. Ostwald also contributed in a significant way by a more critical analysis of the physical factors involved in floating and by making the attempt, at least, to introduce the method of experiment. Woltereck's greatest contribution, undoubtedly, was in his classical study of the dynamics of locomotion of Daphnia, Bosmina, etc. (1913). He changed the aspect of the problem for active plankters from one in which statics too greatly predominated to one in which dynamics received proper consideration. It was not a question of how the animal is prevented from sinking in spite of its weak efforts to keep in the upper water, but rather one of how the animal keeps moving in a generally horizontal direction in spite of its own powerful strokes tending to force its head end upward and backward or vice versa, how it moves along under control at the preferred depth instead of vainly turning somersaults. Keels and rudders afford the answer. It is a fact, however, that the animal gets along in winter with greatly reduced keels and rudders. If the directive processes are necessary adaptations, the necessity must be far greater in summer than in winter. This seems to lead us back to temperature and to some associated quality of water that affects movement through the water—presumably density or viscosity.

Woltereck has evidently made extended use of the experimental method in breeding and rearing Daphnias, but, with respect to many questions, the results of his experiments cannot be effectively and critically availed of by others for lack of knowledge of the condition and precise results of his experiments. We should like to know if the animals were reared in isolation or in mass cultures, the precise temperatures employed, the number of animals used, and other conditions of the experiment.

As we have seen, he emphasizes the great part played by nutrition, and stresses also the function of "generation number" in giving a variable "helmet-potency," "spine potency," etc. At times he relegates tem-

perature to a position of insignificance, at others, as in connection with the Reactionsnorm, he seems to give it more importance. To determine the Reactionsnorm of a race there are required, he says, knowledge of its responses to low, middle, and high nourishment, at low, middle, and high temperatures and in early, middle, and late generations. To what extent are the several conclusions based upon 27 ($3 \times 3 \times 3$) strictly controlled and parallel series of experiments?

Woltereck has also introduced the conception of Präinduktion referring to the indirect influence upon the young of conditions to which the mother had been subjected long prior to the formation of the eggs from which the new generation is derived.

Cyclomorphosis of Daphnia in Relation to Heredity and Evolution

The genetic factors involved in cyclomorphosis are, of course, not disregarded. Heredity determines the particular pattern of cyclomorphosis displayed in a particular population (compare *b* and *c*, fig. 1). In fact it is only a modest exaggeration to say that there are as many hereditary patterns as there are waters inhabited by cyclomorphic forms. The respective winter forms of different lakes may be indistinguishable, although, if collections are made in summer, an almost infinite diversity of forms is found, each form characteristic of the lake in which it occurs. It repeats itself in successive summers and apparently, to an extent at least, in experimental cultures. Woltereck holds that the pattern is modifiable (to the eye) only after a considerable number of generations when the new pattern, a *dauermodification*, or else a *differentiation* becomes more or less definitely fixed in heredity. We need not go farther into this question now except to suggest that a promising field of investigation by experiment is indicated.

The genetic aspect of the general problem of cyclomorphosis leads naturally to the question of the origin of the multitude of summer forms. How has it come about that populations of particular lakes have in season particular forms of genetic validity—say, helmets that are upturned or downturned or directed straight ahead, long or short, rounded or pointed, etc.? We have no occasion now to go into the broad question of phylogeny, although it should be remarked that Woltereck, who probably has a wider acquaintance with limnetic Daphnias of the world than any one else, seems to regard both natural selection and mutation as influences of secondary importance in the origin of the several species and subspecies with their distinctive patterns of cyclomorphosis, holding rather that the environment is of controlling evolutionary effect:

"Alteration of racial qualities in daphnids is either caused or directed by certain environmental factors" (1932).

Other Investigations

The work of some other investigators can be mentioned only very briefly. Langhans (1909), working with 3 non-pelagic species, *D. magna, pulex,* and *obtusa* and the limnetic *D. longispina,* found an inverse correlation between the accumulation of waste products (due to crowding) and both productivity and length of spine. Isolation led to greater egg production and a longer spine. Much earlier, Warren (1900) had experimental evidence that the accumulation of waste products, even in the presence of abundant food and oxygen, led to reduction of spine length for *Daphnia magna* and ultimately to general ill-health, cessation of reproduction, and finally death. Water long inhabited by Daphnia was injurious to fresh Daphnia but not to other Entomostraca—Cyclops and Cypris. In time the water purified itself without treatment and became a suitable medium for new Daphnia.

McClendon (1910), working with *D. pulex,* a species of only moderately pelagic habit and displaying relatively little cyclomorphosis, found nutrition the most important factor, reducing body length and the duration of development but increasing the length of the spine; high temperature, which he regarded as an adverse condition, and starvation have like biological effects. High temperature, then, had an effect in the reverse direction from that noted by others for the more strictly pelagic Daphnias. No effects were gained from the use of various salts in the strongest tolerable concentrations nor from the use of diverse intensities of light and darkness.

Wagler (1913), following Woltereck, related length of head to sexual periodicity. Examples taken in July, a time of reduced abundance, have shorter heads than the more numerous individuals of spring and fall. In a later work (1923) he made what seemed a most telling criticism of the temperature theory when he pointed out that the helmets are generally shorter in small ponds with relatively high temperatures while the longest helmets occur in the larger lakes with lower temperatures than those of ponds. Since he refers to the active metabolism and the excess of food in small ponds, the same argument might have been applied against the nutrition theory. Wagler emphasized stratification, a summer feature of lakes, as the significant environmental factor.

At the same time, Gruber (1923) found a direct correlation between lengths of horn and of mucro in *Scapholeberis mucronata* and the size of the body of water. *Scapholeberis* lives commonly on the underside of the surface film and therefore would not seem to be affected by stratification. It is not clear how stratification of water could act as a direct stimulus. Larger helmets were found also in geologically older waters. Gruber, then, brings in both *size of water* and *geological time* as factors in helmet development.

Schubert (1927) says that if the helmet of *D. cucullata* (very closely related to *D. longispina*) were a function of temperature, we should find the highest helmets at the highest temperatures and the lowest at the lowest temperatures, but his observations in certain lakes indicate that, although there is but one peak in the temperature curve, there may be one, two, or three in the curve representing lengths of helmet, corresponding in his opinion with the three reproductive cycles of the races in question. Therefore temperature is not the primary cause of the modification. Correspondingly, it could be argued, although Schubert does not do so, that if nutrition were the primary cause of helmet formation, the longest helmets should be found in the richest waters and, in any given water, at the time of greatest richness; but is this the case?

Wesenberg-Lund has strongly maintained his position with respect to the significance of temperature in cyclomorphosis. "The seasonal variations do not proceed evenly throughout the year, but by abrupt changes, which are accomplished in the period from the end of May to the middle of July and in Sept.–Oct.; in both cases when the temperature is ca. 14–16°C. The transition can in spring be accomplished in the course of ca. a fortnight" (Wesenberg-Lund, 1908, p. 189). It occurs simultaneously in all lakes (in Denmark) at the same temperature. Furthermore, the change occurs chiefly from generation to generation rather than during individual lives (according to variable food supply). "The outer conditions," he says, "must thus be assumed to act upon the individuals mainly during development of the embryo, less throughout growth, and least after the egg-producing stage" (1908). It is significant that there is no cyclomorphosis in northern lakes where the temperature does not rise to 16° (1910). He had first thought of seasonal variation in form as due to variation in nourishment, but abandoned the supposition because the variation in food supply could never be of such regularity as to bring about such "harmony" of change in the same lake from year to year, in all the lakes of the region and all

the different cyclomorphic organisms. Food supply might be the agent to make the change possible but not the driving force (1926). (This distinction, in connection with the preceding argument, does not seem of clear validity.)

In brief, then, where Wesenberg-Lund and Ostwald would make temperature, through its effect on viscosity of the medium, the controlling factor for change of form, Woltereck sees a double control in the external factor of condition of nutrition and the internal factor of position in the reproductive cycle (helmet potency or "labilität"), heredity, of course, giving the pattern in any case. It is the contention of the adherents of Woltereck's view that, if temperature were the controlling factor, the greatest helmets should be in the warmest waters, which is not the case. On the other hand it is the equally valid objection of Wesenberg-Lund (1926) that if nourishment were the primary regulator, the greatest helmets should be found where the food is richest, which, he says, is not the case. Wesenberg-Lund also questions the correlation of stratified food supply and helmet development, which seems to be an important part of the theoretical base of Woltereck's explanation of the origin of helmets. We are dealing with a phenomenon that manifests itself most conspicuously in the open areas of lakes where the waters are relatively cool and the food may be relatively scant. In ponds where the waters become very warm and the food may be very abundant—it is precisely in such waters that cyclomorphosis does not occur in any prominent way. The novice might assume, then, that there is no controlling factor, or that, if there is, it has not yet been pointed out.

Yet, as Wesenberg-Lund says with respect to the bodies of water in which cyclomorphosis manifests itself: when the water warms up the helmets and extensions appear, and when the water cools off they disappear; this, if it be a general rule, must have some meaning.

In our experiments we have attempted to see what changes in form could be effected by mere change of temperature, and we have made use of an animal that displays a seasonal change of form, not so radical as that of *D. cucullata*, but yet quite marked. Our animal has a special advantage for experimental work, in that the extension of the head characteristic of the summer form is a *positive* acquisition. Mathematical measurements are helpful in respect to the degree of its development or in conveying information to others, but one can tell at a glance if the point is present (however small) or absent (see fig. 4, second row, and fig. 7).

II. OBSERVATIONS AND EXPERIMENTS

The Animal in Nature

Our material was derived from a relatively new artificial lake formed near Chapel Hill, N. C., by the repression of three streams just below their junction. The lake is narrow, its several arms one to one and a half miles in length, but not exceeding a quarter of a mile in width, the area only some 200 acres, the depth near the dam, where all our collections were made, about 20 feet. The lake is distinctly immature, having been formed in 1932. The predominant plankters are *Daphnia longispina, D. pulex, Cyclops leuckarti, C. prasinus* (?), and the rotifers Notholca and Conochilus. Calanoid copepods have not yet appeared. The Daphnia studied and employed in the experiments is provisionally

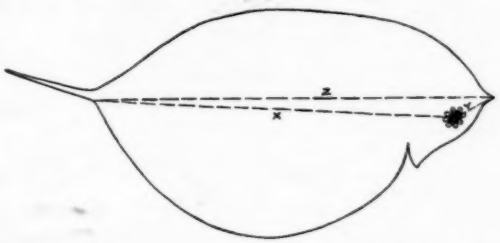

FIG. 3. Showing mode of measurement; see text below

called *D. longispina.* Being without an ocellus it should perhaps be called *longiremis,* but it is at least of the *D. longispina galeata* series belonging to the group of species or subspecies of which *cucullata* forms the terminal series.

For each set of measurements 50 animals of medium size (.70 mm. ±.08 mm.), taken at random, were sketched in outline with camera lucida and measurements made on the sketch from the center of the eye to the front of the head (Y) and from the center of the eye to the base of the spine (X) (fig. 3).

In a collection of January 24th, 1934, all examples were round-headed (fig. 4) as is regularly the case in winter (from observations at various times during five winters), and the quotient of $\frac{Y}{X}$ was 0.10. Daphnia were then scarce, constituting only 8 per cent., by number, of the net zooplankton. On April 5th, Daphnia were more abundant, representing 82 per cent. of the net zooplankton and occurring in both round-head

and pointed-head forms (fig. 4, second row), the latter predominating in the ratio 44:38. The quotient of $\frac{Y}{X}$ for round heads was again 0.10

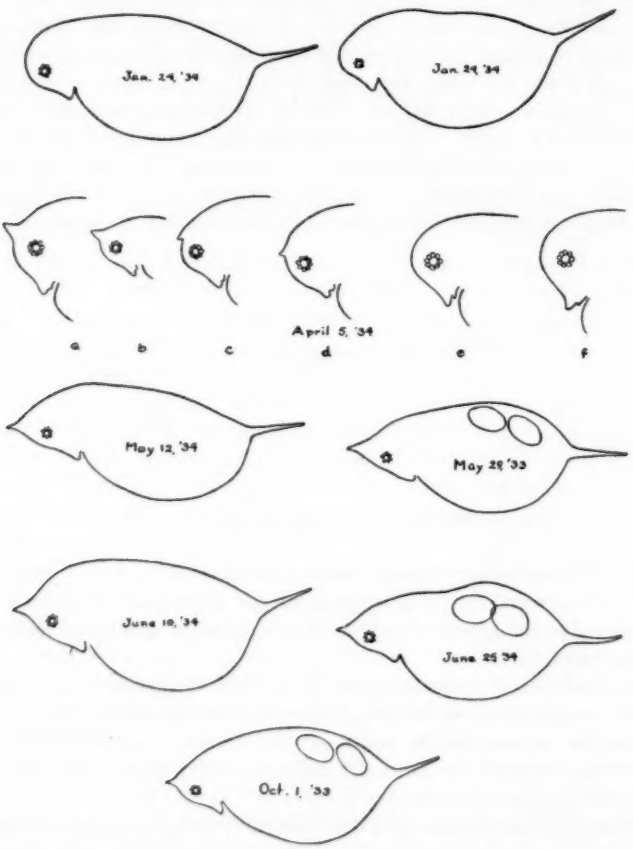

FIG. 4. Illustrating cyclomorphosis of *Daphnia longispina* in University Lake, Chapel Hill, N. C.

and that for pointed heads was 0.144. On May 12th, and thereafter, only pointed heads were found (fig. 4, third row). The quotient of $\frac{Y}{X}$

May 12th was 0.209, showing a much greater development of the point than was found early in April. A collection made in May of the preceding year gave a generally similar result with $\frac{Y}{X} = 0.18$. Three collections in June made on the 10th, 23rd, and 25th (fig. 4, fourth row) gave quotients of 0.192, 0.191 and 0.199, respectively. Larger examples have the helmet relatively less well-developed (fig. 5).

It is evident, then, that the extension of the head before the eye is practically doubled in late spring as compared with the condition in

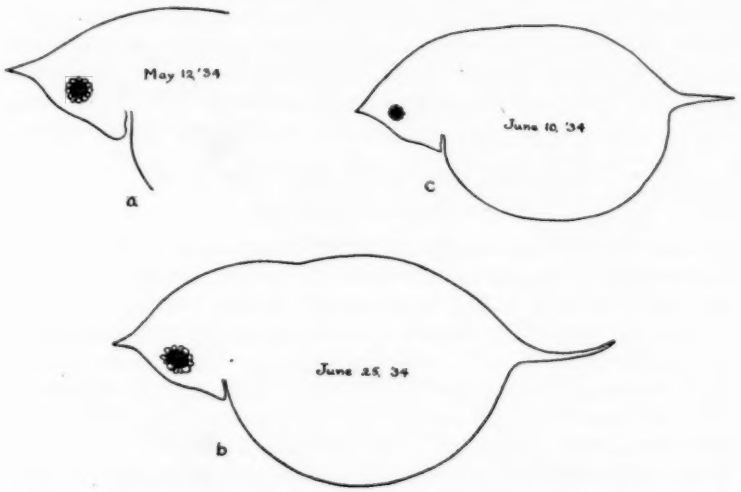

FIG. 5. Showing extreme helmet development (a); older Daphnia may retain pronounced helmet (b); but generally have shorter ones (c).

January, but there is no increase in length of helmet in early summer. Since a collection made on October 1st of the preceding year included Daphnia with strongly pointed heads (fig. 4, bottom), the quotient $\frac{Y}{X} = 0.185$, and round-headed Daphnia were found a little later, there seemed to be a definite cycle, which could be stated as follows: In winter only round heads; in late spring and early summer only strongly pointed heads until disappearance of the species; in early spring and fall both types occurring together, with the points in spring not appearing in

fullest development until late in the season. Such a rule would commend itself for simplicity and for conformity with the facts during one year. It does not, however, conform exactly with the facts of suc-

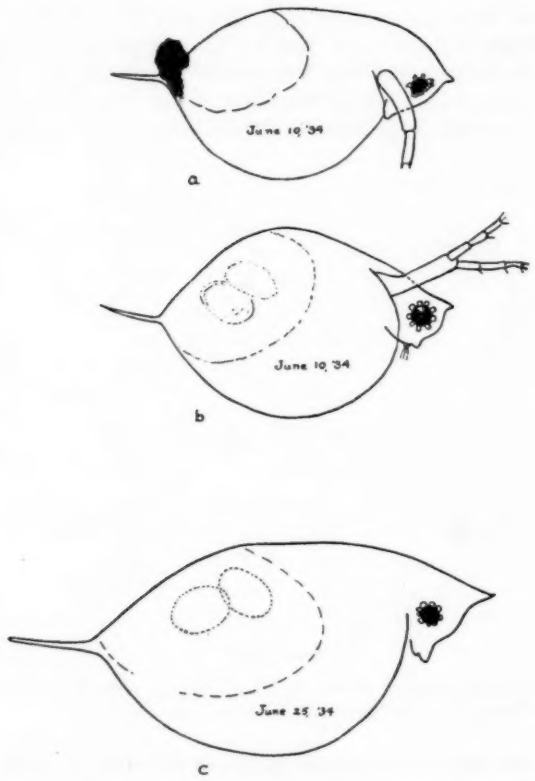

FIG. 6. Stages in development of ephippia, University Lake, June, 1934. The particular animals, especially *b*, are evidently in bad condition; such animals are very rare in the lake and have never occurred in cultures.

ceeding years. During 5 successive Januaries, there have been found only round heads, and the species seems always to disappear or become very rare in midsummer—how or why we do not know since ephippial females (fig. 6) have been found but rarely and about as frequently in

November as in June. In the autumns of 1934, 1935, 1936, and 1937 (in contrast to the condition in 1933) pointed heads were very rare, and particularly so in the early collections when the water was still relatively warm—up to 20°C. or more. Furthermore, in 1935 about two-thirds of the Daphnias were helmeted by March 29th, but a fair proportion of round heads persisted as long as there were Daphnias in the plankton or up to the end of June.

The rule as to seasonal polymorphism is, therefore, only a rough approximation. The correlation with temperature has failed in early fall in every year but one, and it failed partially in the late spring and early summer of 1935. It will appear later that there are difficulties in reconciling the results of experiments in the laboratory with the results of observations on collections in the lake.[3] Hardly a better illustration could be found of the necessity of checking results gained in the laboratory against observations in the field.

The Animal Under Conditions of Experiment

Materials and Methods

The experiments conducted with Daphnia derived originally from the lake were comprised chiefly in 5 series: (1) Addlestone's "straight-temperature," (2) his "transfer" experiments (1934), (3) Coker's straight temperature, and (4) his transfer experiments (1935), and (6) Taylor's straight temperature experiments (1936). The straight temperature experiments were those in which the parthenogenetic animal was kept under a fixed or relatively fixed temperature during at least the whole period of incubation of a clutch of eggs. The transfer experiments were those in which the animal was transferred from one temperature chamber to another so that developing eggs or young were subjected to different temperatures at different times during the period of development. Coker's experimental lines (chiefly three: Nos. 6, 8, and 14) were derived from round-head parthenogenetic females collected in January; Addlestone's and Taylor's from a laboratory stock originally derived from animals collected in the fall—the original females having pointed heads in Taylor's case, uncertain in Addlestone's. Since ephippial females have rarely been found, stem mothers could not be used.

The cultural methods employed by the senior author are described; those of the others were essentially the same, except that in Taylor's

[3] Miss Patty Hill assisted in study of the material from the lake.

experiments overfeeding was deliberately practiced but with generally deleterious results. Mass cultures were never employed; more impressive numbers could be obtained by their use, but only with an undesired complication of environmental factors through accumulation of waste products and in other ways.

Parthenogenetic females, or young, were isolated in shell vials (or in a few cases in large vessels) provided with culture medium made up of filtered aquarium water (rarely of filtered lake water), to which was added a few drops from a protozoan culture and an alga culture (generally Ankistrodesmus). The protozoan cultures were derived in the following way. Several quart jars of stock culture were regularly on hand, made up by filling the jars about one-fourth full of dried horse manure or sheep manure and adding filtered aquarium water to near the top. The culture ripened in a few days. Every few days each of these was examined to select the one that contained the most nearly pure culture of minute protozoa—Chilomonas or other protozoa of small size. It has been observed that large infusoria, such as Paramoecium, clog the filtering apparatus of *D. longispina*, causing a temporary interruption of the feeding process while the large infusorian is "kicked out." With a pure culture of Chilomonas a continuous stream of food may be observed to pass into and along the alimentary tract of a Daphnia lying on its side in a drop on the slide. The mandibles of *D. longispina* have good teeth, but for what purpose they are used has not been observed.

The stock culture for use having been selected, a quantity of the medium was passed through medium fine filter paper into a 100 cc. bottle to which was then added a pipette or two of the pure cultures of algae; the filter eliminated debris, and most of the larger protozoa. Feeding was done from the best of the filtered media, several of which were always at hand. One might be good for a day only; another would continue productive for several days.

When young were born each was placed in a separate drop on a slide and examined under the microscope for form of head. Each one to be used for breeding purposes was then placed in a shell vial to itself with about 20 cc. of filtered aquarium water to which was added enough of the food culture (2–10 cc.) to give a slight cloudiness to the water. Examination and feeding was done every day at 20°, every other day or oftener at 12° to 16°, and at least every third or fourth day at 9°. From the record kept for each culture, birth could usually be anticipated within a day and supplemental examinations made accordingly. About once a week, or a little less frequently at lower temperatures, the entire medium in a culture vial was changed.

We did not attempt to control all conditions of the experiment—food, oxygen, carbon dioxide, etc. What we did was to keep the one influence, *temperature*, under control (roughly in first experiments, more precisely in the later ones), letting the other possible sources of influence (except light and size of container) be moderately variable, and then to check the consistency of the results as the experimental factor was changed.

Experiments with "Straight" Temperature

When the first series of experiments were conducted by Addlestone in 1934, apparatus permitting accurate temperature control was not available. The following temperature conditions were utilized: (1) A cold room used for other purposes, in which the temperature was generally 4–5° but occasionally a degree higher or lower; (2) a water bath with running tap-water, its temperature at first fluctuating between 8° and 13°, but rising in the latter part of the season to 16° (no individual experiment was, however, subjected to a range of more than 4 or 5°); (3) a basement room in which the temperature fluctuated from 18 to 23°, and rarely to 25°; (4) an oven with temperature nearly constant at 28°. At each place temperature was recorded three times daily.

Since all Daphnias reared, whether born with round or pointed heads, became round-headed in course of development, and, in every case, except two, before attaining sexual maturity, we may refer for the present only to the *form of the head at birth*. In the cold room (5° ± C.) 31 round-head young were liberated; in the water bath in the early part of the experimental work (8°–13°C. and generally below 13°) 100 round heads and no pointed heads appeared; in the basement room (20° ± C.) 160 pointed heads, and in the oven (28°C.) 61 pointed-head young were liberated. Thus we have 131 round-head young at low temperatures (below 14°C.) and 221 pointed heads at high temperatures (about 18°C.). In many instances (11 at least), the same parent was allowed to produce young at low and high temperatures in alternation, but the form of the head in the young corresponded without exception to the temperature rule just indicated. There were, however, 4 broods, in addition to those mentioned, in which both forms of heads appeared, and these were born at temperatures of about 14° or above, but well below 18°.

The following tentative conclusion seemed justified: The form of the head of the young is subject to control by regulation of temperature and the critical temperature is somewhere in the vicinity of 14°, at least between 12° and 18°C.

It was desirable, of course, to have more precise control of tempertures below room temperature, but we did not find on the market an apparatus of sufficient flexibility and convenience of form. With the aid of Dr. E. W. Constable, a new apparatus was devised to give precise and continuing control to a tenth of a degree at any desired temperature and permit several temperatures to be maintained simultaneously (Coker and Constable, 1936). Another series of experiments was then conducted by the senior author with results on the point in question as given in Table I.

These results conform with those of the preceding series of experiments as to the general level of the critical temperature for change of head

TABLE I

Numbers of Daphnia longispina born at several constant temperatures and percentage with pointed heads at birth

TEMPERATURE[1]	TOTAL NO. BORN	NO. WITH ROUND HEADS	NO. WITH POINTED HEADS	PERCENTAGE WITH POINTED HEADS
°C.				
9	58	58	0	0
11	196	194	2	1
12	116	99	17	14.7
13	75	50	25	33.3
14	55	7	48	87.3
16	32	0	32	100.0
20	101	0	101	100.0
	633	408	225	

[1] For present purposes, temperatures are stated in even figures. That in some experiments the bath may have been set at 0.1° or 0.2° above or below the even figure is immaterial in this discussion.

form. They show, however, that there is not a sharply defined critical point on the temperature scale, applicable to all breeders or young, but rather that, under the conditions of the experiments, the critical temperature varied between 11° and somewhere below 16°. Subsequently Taylor, in connection with experiments having a different objective, observed 45 young born at 21.6° and 60 born at 15.1°, all with pointed heads and 11 born at 11.1° with round heads. The critical range is narrowed from 11° to 15°, centering apparently, at a little above 13°.

Conditions of food supply may have had some effect in shifting the apparent critical temperature in some cases in one direction or the other, but it seems highly improbable that three different experimenters, in

three different years, with a number of different stock food supplies, should have attained results in such close correspondence with respect to the same experimental variable, if that common variable (temperature) were not a highly significant one. In fact, in connection with other studies, many other Daphnia have been bred in the laboratory at temperatures sometimes below and sometimes above the critical range, and exceptions to the rule simply do not occur.

It may be recalled that breeders were kept in individual vessels, abundantly fed, and protected from excessive accumulation of waste products. It is to be noted here that Wesenberg-Lund (1926), after many years of observations in the field, found that the change of form of wild *Daphnia cucullata* in lakes of Denmark occurred in early summer, soon after the temperature of the water rose to about 12–16°C.

FIG. 7. Illustrating least development of helmet as "bump," "angle," or hook. Contours of brow of Daphnia bred at 12°C., although round heads are the rule at this temperature.

Since we find both pointed and round heads appearing at temperatures within what may be called the critical range, it may be of interest to examine more closely the broods reared at 12°, 13°, and 14°C. in the second series of experiments where temperatures were precisely controlled throughout the course of each experiment.

The 23 clutches of 3 lines born at 12° were either all round heads or mixed, embracing some with clearly rounded heads, some with slight but distinct points, and some with mere bumps (fig. 7). Only a single clutch had no round heads, and that comprised but one individual with small point. Not one animal in any of these clutches had marked points. At 13° mixed broods predominated (9 out of 15) and 3 comprised exclusively pointed heads. At 14°, 13 of 18 clutches were made up exclusively of pointed-head young in which the points might be very

insignificant or sometimes quite large; there were only 3 mixed clutches and 2 having 1 round head each. In the mixed clutches at 13° and 14°, and in the purely pointed-head clutches at 13°, the points were all very small and sometimes mere "bumps." Even at 16° (11 clutches), about half of the points were small, whereas at 20°, only 6 of 101 points were described as "small" (but not insignificant), while most of them were very pronounced.

There was no evidence from rate of growth or size of broods to indicate that deficiency of food was associated with roundness of head. In fact, the average number of young in the clutches was notably greater at lower than at higher temperatures, being 8.3 at 9°, a little over 5.4 at 11°, 5 at 12° and 13°, 3 at 14° and 16°, and 4 at 20.°[5] The numbers are not now considered significant except in a negative way, as offering no evidence of superior nutritive conditions where extension of the head characterized the newborn.

With respect to the 3 lines employed in Coker's experiments, there was apparently not half a degree of difference in the responses of the several lines to temperature.

Transfer Experiments

These experiments were made to determine the effect on the developing eggs or embryos of a change of temperature during the period of development. Addlestone made 27 transfers of parthenogenetic females (15) from one temperature to another involving 30 clutches born under conditions of transfer, besides 15 born before transfers. In all 97 young were born after transfer. In 14 cases (44 young) where the eggs were passed into the brood pouch after the transfer, there was no evidence at all of an influence of the original temperature on the form of the young; 12 cases (41 young) where the transfer was made late in the incubation period the young had clearly the form corresponding to the second temperature. The exact critical period in incubation was not discovered.

In another series of experiments the senior author made 35 effective transfers of females with young in the brood pouch. (A good many transfers are ineffective, because the young are not infrequently aborted and lost with severe change of temperature.) The following landmarks in development were noted:

[5] Contrary to Ostwald's view that low productivity with low temperature is the rule.

(1) New eggs in brood pouch
(2) Eggs hatched (the shells are cast early in development)
(3) Head outlined
(4) Advanced embryos with appendages showing
(5) Two-eyed embryos
(6) One-eyed embryos
(7) Young liberated ("born")

In general the results from all transfers, with a total yield of 195 young, correspond to the rule that the new temperature is ineffective as to form of head after the distinct appearance of the two eyes, whether the transfer was from a lower temperature to a higher or the reverse. There were, however, a few exceptions that may be significant. In two cases of transfer from 16° to 13°, with "hatched eggs" in the brood pouch, when the expected form would have been that of 13° (with no points or with only insignificant ones), 2 of 7 and 4 of 5 young had notably larger points. In a 9°–20° transfer, 2 young moved to the chamber of higher temperature before the appearance of eyes, had round head and "angled" head, respectively, instead of pronounced points. A female with "hatched eggs" transferred from 12° to 20°, yielded 3 young with small instead of large points. Probably the most notable exception was a clutch of 5 young born at 20° after transfer in the stage "head outlined:" 1 of these had a round head, and 4 only tiny points or angles, where prominent points might be expected.

Two clear exceptions and 14 partial ones do not constitute an impressive number of exceptions, but these do suggest that there is an influence of temperature during the early part of development, which is usually, but not invariably, overruled by the influence of the conditions surrounding the embryo during intermediate stages of development. It may be remarked that Ostwald (1904), from two chance observations of gravid parents transferred from the room to the cold bath at 3 and 4 days, respectively, before liberation of the young, when the young in the first case had somewhat longer heads than the mother and those in the second case had somewhat rounder heads, concluded that the form-determining influence of temperature takes effect only between the third and fourth day of development, or at the beginning of the second half of the period of incubation. The evidence was meagre and might have been interpreted more logically as indicating that temperature ceases to exert an effective influence after a certain critical stage. He was nevertheless correct in suggesting that with respect to the influence of temperature there was a critical stage in embryological

development which could be determined more accurately only by further experimentation. Our observations suggest that the critical stage *beyond which temperature is ineffective* is somewhat variable but generally at the stage marked by the appearance of the 2 primitive nauplial eyes.

Finally, it may be noted that the transfer experiments confirm the straight temperature experiments as to the influence of temperature on form of the newborn, merely fixing more definitely the time of action as being after the eggs are in the brood pouch and before a certain stage in embryonic development has been attained. The 195 young bred in these experiments may, therefore, be added to the 1116 reported in preceding paragraphs, making the total young liberated at various temperatures 1311 (besides others not here listed) without a single clear exception to the inferred rule of correlation of form of newborn with temperature; the few exceptions to the "rule" as to critical period in development are not, seemingly, exceptions to the general rule of correlation.

There seems, then, to be a definite influence of temperature, as it acts on the animal itself and not upon its food supply. It may be said, of course, that it is the effect of temperature on the assimilation capacity of the animal, but this, after all, is a direct effect on the animal. Neither Wesenberg-Lund nor Ostwald have suggested that temperature acts, directly or indirectly, except through an influence on the metabolic activity of protoplasm. The influence on the young might, however, be direct (in this sense) or it might be indirect through the mother, which under different conditions of temperature could contribute to the developing eggs or embryos different quantities or qualities of nourishment in consequence of changes in her own metabolic activities. Let us now examine this question.

All of the experiments indicate that prolonged subjection of a female to either low or high temperature has no appreciable effect on eggs laid at a new temperature as regards the form of the head of the young hatched from them. There is no Präinduction in the sense of Woltereck, as regards form of head at birth. It seems clear that the influence is exercised chiefly during intermediate stages of development of the embryo.[6] It might still be that the embryos are affected, not directly

[6] It is assumed by some investigators that temperature, or some other condition, is effective only when it leads to the formation of a helmet. Unless there is a fallacy in our reasoning, the round head is as much a product of the interaction of internal and external factors as is the pointed head; low temperatures may be as positive in action as high temperatures.

by the temperature, but by something furnished by the mother as a secretion from the lining of the brood pouch. For more than half a century the brood pouch of Cladocera in general has been commonly assumed to be a sort of uterus into which the mother secretes necessary nutritive substances; but Rammner (1933) finds that with several species of Daphnia and Simocephalus, the eggs develop just as well if removed from the brood pouch in a very early stage of development, even before they are hatched; in Moina, Leptodora, etc., the case is different—the pouch is a uterus. During the past year I. S. H. Metcalf, a student in our laboratory, succeeded in having a small number of new eggs that had been removed from the brood pouch complete their development in depression slides or hanging drop cultures. The form of the head at the stage of normal "birth" corresponded with the temperature at which the eggs were kept regardless of the temperature to which the mother had been subjected while the eggs were being formed and extruded into the brood pouch. Exclusive of cases where the temperature of artificial incubation was the same as the temperature at which the eggs had been formed in the mother: there were 9 taken from mothers at 10.2° and incubated at 19.05°—all had pointed heads; there were 3 taken from others at 19.05° and incubated at 10.2°—these developed round heads. One clutch of 7 eggs formed by a mother at 10.2° was divided into two lots: 4 eggs were incubated at 10.2° and 3 at 19.05°; the former developed round heads, the latter pointed heads.

There is clearly no need now to make any other inference than that temperature, acting directly upon the embryos, exerts some influence on growth or multiplication of cells to cause the production of helmets, or points, at temperatures above a critical level that lies around 13°C. (or about a couple of degrees lower or higher with different individuals).

Before, however, we become too strongly impressed with the significance of temperature in the regulation of the form of the head, the facts presented in the next section must be considered.

Loss of Point after Birth

We have noted that temperature seemed to lose its power to influence form after the appearance of eyes in the embryo. This seeming loss of influence may be actual or it may be that there is not time after the eyed stage and before birth for the influence to exert an observable effect. Now it happens that, with all the pointed-head young reared in the experiments of Addlestone and Coker, the point was invariably lost in course of the first few molts; once lost, it was never regained. Therefore, all breeding animals (except 2) were round-head, regardless of the

temperature at which they were born or bred, and the two exceptions, retaining a vestige of a point at the primipara stage (3rd to 5th instar), lost it in the next succeeding molts.

In the experiments of Taylor the loss of point occurred in a similar way, except that in 5 of 29 reared at 15.1° and in 1 reared at 11.1° (but *bred* at 15.1°) the point, although reduced by the 3rd or 4th instar to a vestige, was never lost. Furthermore, in 18 of those reared at 15.1° and in 5 reared at 11.1° (but *bred* at 15.1°) a good point subsequently developed, and in six others at 15.1° a slight hook or an angle appeared. The development of the point during free life cannot well be attributed to temperature but evidence as to the actual cause is wanting. One can only think of something in the surrounding medium. Miss Taylor's animals were, by the way, reared in larger containers. Certainly, in the wild state in the lake the points are not lost, but round-headed Daphnia are either wanting or relatively few during late spring and early summer, a period of great reproductive activity.

As Wesenberg-Lund has pointed out, it is difficult to reproduce in small vessels in the laboratory the conditions to which a pelagic animal is accustomed. We have had the same experience as some others in this—that the majority of wild Daphnia die when brought into the laboratory. Once, however, a line has been established, our *Daphnia longispina* have showed a most satisfactory adaptation to our cultural conditions. Fertility and viability have improved with succeeding generations. Sixty days or more was not an uncommon duration of life: the maximum was 88 days and some might have lived longer but for the termination of the experiments. The number of clutches from one female varied from 1 to 8. The numbers of young per clutch, although always small 1 or (2) with the primiparae, was with older breeders often 10 and occasionally 13 or 14. The number of generations in a line (7, the maximum) was limited only by the duration of the experiments. Evidence of lack of adaptation might be found in the fact that sometimes an individual would go for a long time without extrusion of eggs, when one or two complete changes of medium would be followed by active egg-production. Never, however, in such cases, did the form of the head of the young born from such eggs reveal any influence of conditions other than temperature. Never also was there evidence of "Depression" in production of males or ephippial females.

The possible influence of *light* is of course to be thought of. In the senior author's experiments all culture vessels were in the dark, so that light could not have been a factor in producing the change from round to pointed heads.

Generation Number and Präinduction

Woltereck reports a remarkable difference in the responses of *D. cucullata* to external conditions in the first and sixth generations (fig. 2). Our experiments offer no support to that view. The negative evidence of our experiments on this question may perhaps be subject to some discount, since we bred only 7 generations from a wild generation of unknown number. Nevertheless, the regularity with which the form of the head of the newborn in a number of series of experiments (including several not mentioned here) is found to conform to a rule of correlation of head-form and temperature during incubation makes it seem quite unlikely that the place of the individual in the hypothetical reproduction cycle has anything to do with the response. Furthermore, evidence gained by several investigators previously cited tends to discredit the significance and even the existence of a "reproductive cycle."

In the lake, the last parthenogenetic generation certainly shows no loss in capacity to form helmets (see fig. 6 *c* where $\frac{Y}{X} = 0.22$); and that, notwithstanding the fact that some of the animals show signs of "Depression."

As to Präinduction, or the effect on the *germ cells* of the embryo in the brood pouch of the mother, carrying the hypothetical control back one complete generation, our evidence is decidedly on the side of the negative.

Comment

So extraordinarily complex are the form relations of pelagic Daphnia, where every lake seems to have its own particular race, as Wesenberg-Lund and Woltereck have found (notwithstanding that change of form in spring, and sometimes in fall, synchronizes roughly at least with temperature), that it would seem foolhardy to attempt now to apply any simple explanation to the whole phenomena of cyclomorphosis. Wesenberg-Lund (1926) describes a race of *D. longispina galeata* in which the young at all seasons are born with round heads, while the mature animals show a marked elongation of the head in summer; and another in which both round and pointed heads occur in winter (and this in Denmark) but the points are high and sharp only in summer. Again he compares two races of *cucullata* from waters less than half a kilometer apart, a lake and a pond with insignificant difference of temperature. In the lake a marked cyclomorphosis extends through the summer; in the pond a dwarfed but heavy race begins a cyclomorphosis

in June, but in July the crest diminishes until typical round heads appear in August. In midsummer there is a maximum of numbers in the lake and a minimum in the pond; this suggests that nutrition could be a factor, but Wesenberg-Lund thinks it highly improbable that the dwarf race is a result of starvation, although he says there must be something with respect to assimilation to cause the decrease in length, in crest, and in numbers for the race in the pond, just when the race in the lake attains its maximum in all these respects. In both waters the number of eggs per clutch is reduced at this time to 1 or 2, which does not suggest a strong contrast in nutritive conditions.

From field observations, Wagler (1923) suggested that the high temperature and abundant food-supply of ponds promotes rapid development, maturity at small size, and small crests, and the lower temperature and poorer nourishment of lakes, a slower development, larger size and higher crests. He recognized that this seemed to conflict with the experimental data, but suggested no means of reconciliation. His suggestion does not appear, either, to fit the sequence of events in a given lake.

It seems impossible to escape the conclusion that, under the conditions of our laboratory experiments, temperature controls the form of the head of the newborn,[7] but does not control that of the free-living. In the lake temperature does not constitute a sufficient explanation, but is probably involved. In both cases it is probably temperature *plus*. In another paper (1939?) we have discussed the "plus" factor which may be a positive (promotive) or a negative (inhibitory) one. Without repeating that discussion, we may allude here to the results previously obtained by Warren and Langhans and cited p. 52 above. These data do not, however, offer a good parallel to our results, since in our cultures the loss of helmets was unaccompanied by detectable signs of

[7] It may not have a direct bearing, but the work of H. R. Seiwell (1930) in our laboratory on the heart-beat of a related Cladoceran, *Simocephalus vetulus*, ought not to be overlooked in this connection. In that study it seemed clear that there was a "critical temperature" for rate of action of the heart in the neighborhood of 13°. The heart of *Simocephalus* and the form of the head of Daphnia are not the same thing, but the two animals are very closely related, originally of the same genus. Between 12° and 14° something happens in *Simocephalus* to cause a notable change in the response of the protoplasm of the heart to conditions of temperature; between 12° and 14° something happens in Daphnia in the protoplasm of head-forming cells to effect a notable change in the response to temperature as respects the relative rates of growth or multiplication. There may be something in the idea of a critical temperature for Cladocera at about 13°.

ill health or loss of reproductive capacity but rather, generally, by a naturally growing reproductive efficiency.

Finally it should be emphasized that the experimental conditions have not given us any form of head that is not in character with forms displayed by the wild Daphnia. We have obtained head forms in considerable diversity but all conform to the genetic pattern. Experimental conditions determine only the appearance or non-appearance and the degree of development of a structure the general nature of which is fixed by heredity. We get smaller or larger University Lake helmets, or no helmets, but never, for example, a Chautauqua Lake helmet (contrast fig. 1*c* with all other figures).

The problem is complex, as might be expected. We have attempted an experimental attack on one phase of the problem, and the following conclusions seem justified.

CONCLUSIONS

1. The form of the head of the race of *Daphnia longispina* in University Lake shows seasonal variation, only round heads appearing in winter and chiefly prominently pointed heads on young and old in late spring and early summer. Mixed populations of round and pointed heads are present in early spring and in mid-autumn. At first in spring the points are small, but, so far as we have observed, the fullest development of the head is attained by early May and no further expansion occurs thereafter. A strict correlation with season or with temperature seems to fail, since some round heads have been found in June and a whole population of round heads in September, when the water is quite warm.

2. In the laboratory the critical temperature for form of head of the newborn is about 13°C., but developing young subjected at a proper time during incubation to a temperature a degree or two above or below 13° may have round heads or heads with minute points or angles. At temperatures below 11° only round heads, and above 15° only pointed heads are developed. Young incubated at 16° have marked points, at 20° usually much more prominent points.

3. The form of the head, pointed or rounded, of newborn in the laboratory is determined by the temperature to which they are subjected during intermediate stages of development. Change of temperature after the 2-eyed stage has ordinarily no effect on form of head. Possibly the effect of temperature may be cumulative during the early and middle period of development, for there is slight evidence that conditions of

temperature during the early part of the period of incubation have some effect. Presumably temperature acts through an influence on the metabolism of the developing embryo.

4. A few eggs incubated without the brood pouch developed into young with form of head corresponding to the temperature of incubation, not to that to which the parent had been exposed.

5. As a corollary to conclusion (3) with some corroboration in (4), the temperature to which the parent is subjected during the formation of eggs in the germarium, or at any time except during the first two-thirds of the period of incubation, has no effect on the head of the newborn; the conditions to which the grandparent was exposed have no effect: there is no "Präinduction" as regards the form of the head at birth.

6. The evidence as respects abundance of food supply on form of head of newborn is entirely negative.

7. There was no detectable influence of temperature on the form of the head of young in the free-swimming state or on that of sexually mature females.

8. Young born with pointed heads have invariably lost, or almost lost, the point in course of the first few molts, but in a few instances the points have been regained at about the primipara stage (3°–5° instar). Conditions governing loss and recovery of point have not been determined, but it is evident that temperature is not the primary factor. Since Daphnias in the lake at the proper seasons have conspicuous points at all stages, the loss of point in the laboratory must be attributed to some deficiency in the cultural medium.

9. Although at times unfavorable experimental conditions were indicated by the more or less prolonged interruption of reproductive activity, by the formation of imperfect eggs or by the loss of spines, such occasional and supposedly "depressive" conditions never led to gamic reproduction or to change in the relation of form of head of the newborn to temperature. That the experimental conditions were generally favorable is indicated by low mortality, generally long life, frequent extrusion of eggs, and large clutches from older animals.

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BIBLIOGRAPHY

BANTA, ARTHUR M.
1914. Selection of strains of Daphnia with reference to reaction to light. Yearbook Carnegie Institution of Washington **13**: 131.

——— AND L. A. BROWN
1923. Some data on control of sex in Cladocera. Eugenics, Genetics and the Family **1**: 142-149.

1929. Control of sex in Cladocera. I. Crowding the mothers as a means of controlling male production. Physiological Zoology **2**: 80–92.

1929a. Control of sex in Cladocera. IV. Relation between the rate of the mother's development and the sex of the young. Ibid., 302–308.

BERG, KAJ

1931. Studies on the genus Daphnia O. F. Müller, with especial reference to the mode of reproduction. Reprinted from: Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening **92**: 222 pp., 7 pls.

1934. Cyclic reproduction, sex-determination and depression in the Cladocera. Biological Reviews **9**: 139–174. Cambridge.

COKER, R. E. AND E. W. CONSTABLE

1936. A new multiple constant temperature apparatus for experimental work in biology. Journal of the Elisha Mitchell Scientific Society **52**: 27–34.

1939 (?) The problem of cyclomorphosis in Daphnia. (To appear in Quarterly Review of Biology.)

DIEFFENBACH, H. AND R. SACHSE

1912. Biologische Untersuchungen an Radertieren in Teichgewässern. Internationale Revue d. gesamten Hydrobiologie, etc. Biologische Supplement (3), Heft. **2**: 1–94.

GROSVENOR, G. H. AND GEOFFREY SMITH

1913. The life-cycle of Moina rectirostris. Quarterly Journal of Microscopical Science **58**: 511–522.

GRUBER, KARL

1923. Beobachtungen an Lokalrassen der Cladoceren. Internationale Revue der gesamten Hydrobiologie, etc., **11**: 158–172.

KÜTTNER, OLGA

1909. Untersuchungen über Fortpflanzungsverhältnisse und Vererbung bei Cladoceren. Internationale Revue der gesamten Hydrobiologie, etc., **2**: 633–667.

LANGHANS, V. H.

1909. Ueber experimentelle Untersuchungen zu Fragen der Fortpflanzung, Variation und Vererbung bei Daphniden. Verhandlungen der Deutschen Zoologischen Gesellschaft, Leipzig, **19**: 281–291.

MCCLENDON, J. F.

1910. On the effect of external conditions on the reproduction of Daphnia. American Naturalist **44**: 404–411.

OLOFSSON, O.

1918. Studien über die Süsswasserfauna Spitzbergens. Zoologiska Bidrag Från Uppsala **6**: 183–646.

OSTWALD, WOLFGANG

1902. Zur Theorie des Planktons. Biologisches Centralblatt **22**: 596–605, and 609–638.

1904. Experimentelle Untersuchungen über den Saisonpolymorphismus bei Daphniden. Archiv für Entwicklungsmechanik der Organismen **18**: 415–451.

RAMMNER, W.

1933. Wird der Cladoceren-Embryo vom Muttertier ernährt? Archiv für Hydrobiologie, Stuttgart, **25**: 692–698.

SARS, G. O.
1890. Oversigt af Norges Crustaceer med forelöbige Bemaerkninger over de nye eller mindre bekjendte Arter. II. Forhandlinger: Videnskabs-Selskabs i Christiania, No. 1: 1-80.

SCHUBERT, ALFRED
1927. Beitrag zur Analyse der Alters- und Temporalvariation einiger Lokalrassen von *Daphnia cucullata* G. O. Sars. Internationale Revue d. gesamten Hydrobiologie, etc., **18:** 1–74.

SEIWELL, H. R.
1930. Influence of temperature on the rate of beating of the heart of a cladoceran. Journal of Experimental Zoology **57:** 331–346.

SHULL, A. FRANKLIN
1929. Determination of types of individuals in aphids, rotifers and Cladocera. Biological Reviews **4:** 218–248.

SMITH, GEOFFREY
1915. The life-cycle of Cladocera, with remarks on the physiology of growth and reproduction in Crustacea. Proceedings of the Royal Society of London, Series B, **88:** 418–434.

STUART, C. A. AND H. J. COOPER
1932. Food as a sex-determining factor in *Moina macrocopa*. Physiological Zoology, Chicago, **5:** 70–91.

WAGLER, ERICH
1913. Faunistische und biologische Studien an freischwimmenden Cladoceren Sachsens. Zoologica **26**(67): 305–366.
1923. Über die Systematik die geographische Verbreitung und die abhängigkeit der *Daphnia cucullata* Sars von physikalischen und chemischen Einflüssen des Milieus. Internationale Revue der gesamten Hydrobiologie, etc., **11:** 41–88, and 265–316.
1923a. Über die sogennante Temporalvariation der Cladoceren. Verhandlungen der Deutschen Zoologischen Gesellschaft, Berlin, **28:** 55–57.

WARREN, ERNST
1900. On the reaction of *Daphnia magna* (Straus) to certain changes in the environment. Quarterly Journal of Microscopical Science **43** (N.S.): 199–224.

WESENBERG-LUND, (C.)
1900. Von dem Abhängigkeitverhältnis zwischen dem Bau der Planktonorganismen und dem spezifischen Gewicht des Süsswassers. Biologisches Centralblatt **20:** 606–619, and 644–656.
1908. Plankton Investigations of the Danish Lakes. General part. The Baltic fresh-water plankton; its origin and variation. I. Danish Freshwater Biol. Lab. Op. 5: Text, XII + 389. Copenhagen.
1910. Grundzüge der Biologie und Geographie des Süsswasserplankton nebst Bemerkungen über Haupt probleme zukünftiger limnologischer Forschungen. Internationale Revue der gesamten Hydrobiologie, etc., III Biologisches Supplement **1:** 1–44.
1926. Contributions to the biology and morphology of the genus *Daphnia*, with some remarks on heredity. Det Kongelige Danske Videnskabernes Selskabs Skrifter Naturvidensk. og Mathem. Afg., 8, Raekke, XI, **2:** 89–252.

WOLTERECK, R.

1908. Ueber natürliche und künstliche varietätenbildung bei Daphniden. Verhandlungen der Deutschen Zoologischen Gesellschaft, Leipzig, **18**: 234–240.

1909. Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. Ibid. **19**: 110–173.

1911. Über veränderung der Sexualität bei Daphniden. Experimentelle Untersuchungen über die Ursachen der geschlechtsbestimmung. Internationale Revue der gesamten Hydrobiologie, etc., **4**: 91–128.

1911a. Beitrag zur Analyse der "Vererbung erworbener Eigenschaften": Transmutation und Präinduktion bei Daphnia. Verhandlungen der Deutschen Zoologischen Gesellschaft, Leipzig, 20–21 Jahresversammlung (1910–1911): 141–172.

1913. Über Funktion, Herkunft und Entstehungsursachen der sogen. "Schwebe-Fortsätze" pelagischer Cladoceren. Zoologica **26**(67): 474–550.

1920. Variation und Artbildung. Analytische und experimentelle Untersuchungen an pelagischen Daphniden und anderen Cladoceren. Internationale Revue der gesamten Hydrobiologie, etc., **9**: 1–151.

1928. Über die Spezifität der Lebensraumes, der Nahrung und der Körperformen bei pelagischen Cladoceren und über "Ökologische Gestalt.-Systeme." Biologisches Zentralblatt **48**: 521–551.

1930. Alte und neue Beobachtigungen über die geographische und die zonare Verteilung der helmlosen und helmtragenden Biotypes von Daphnia. Internationale Revue der gesamten Hydrobiologie, etc., **24**: 358–380.

1932. Races, associations and stratification of pelagic daphnids in some lakes of Wisconsin and other regions of the United States and Canada. Transactions of the Wisconsin Academy of Sciences, Arts and Letters **27**: 487–522.

WUNDSCH, H. H.

1921. Beiträge zur Frage nach dem Einfluss von Temperatur und Ernährung auf die quantitative Entwicklung von Süsswasserorganismen. Zoologische Jahrbücher, Abt. f. Allg. Zool. u. Phys. **38**: 1–48.

ZACHARIAS, E.

1893. Biologische Mitteilung. Forschungsberichte a. d. biol. Station zu Plön **1**: 27–52.

1894. Beobachtungen am Plankton des Gr. Plöner See's. Ibid. **2**: 91–137.

ANOMALIES OF CRUSTACEAN DISTRIBUTION IN THE CAROLINAS WITH LIST OF CYCLOPOIDS OF THE GENERAL REGION OF CHAPEL HILL, N. C.

By R. E. Coker

With 16 Text Figures

Studies of the fresh-water plankton Crustacea and decapod Crustacea in the southeastern states are very restricted, with the consequences, not only that the crustacean fauna of the region is little known, but also that general accounts of crustacean species and their distribution in the United States are quite imperfect and even, in many cases, decidedly erroneous. It is intended to record here a few observations of more than usual interest, most of which have been made by chance and incidental to other studies.

CALANOID COPEPODS

In another place (Coker, 1938?) we have discussed the crustacean fauna of White Lake, in Bladen County, N. C., with its calanoid, harpacticoid, and cyclopoid copepods appearing far from previously known ranges for the several species or groups of species (*Diaptomus minutus* Lilljeborg, *Epischura nordenskioldi* Lilljeborg, *Cyclops nanus* Sars, *Bryocamptus australis* mihi, *Attheyella wierzejskii* (Mrázek)).

Until *Diaptomus birgei* was taken in Lake James, N. C. (Coker, 1926), Marsh, who was the best authority on American centropagids, regarded that species as distinctly northern and unlikely to be found south of 39°N. latitude, or, say, the latitude of Washington, D. C. (Marsh, 1907). Having found this species as the only calanoid occurring abundantly in Durham City Reservoir, Lake Michie near Durham, and Brant Lake near Greensboro, we suspect now that it is the most common fresh-water calanoid of central North Carolina.

The finding of *Diaptomus reighardi* Marsh in Lake Mattamuskeet, Hyde County, North Carolina, collected by Dr. S. F. Hildebrand near New Holland, N. C., May 8, 1935, and recently identified by Dr. S. F. Light, offers another case of notable extension of range, since the species has hereto been recorded only from the near vicinity of the Great Lakes.

Concerning *Diaptomus augustaensis* Turner, an example of which I collected near Chapel Hill in a bayou off Bolin's Creek, Marsh remarked that it was the only specimen that had ever come to his attention. The bayou has subsequently been destroyed by drainage operations of the municipal sanitary service. This species was previously known only from the type locality, Augusta, Ga., where it was collected and described by Turner (1910). *Osphranticum labronectum* Forbes has been found in the same bayou, as well as in pools across Bolin's Creek from Glen Burnie Farm, in a marsh at the Mason Farm (all near Chapel Hill) and in the impounded Golf Creek near Pittsboro, N. C. Although it is known from Oregon to Washington, D. C., and from Minnesota to Alabama, Louisiana, and Guatemala (Marsh, 1933), the infrequency of its discovery and the irregularity of its known distribution make any local record of significance.

HARPACTICOID COPEPODS

Harpacticoid records in my papers of 1934 and 1938 (?) give great extension of range for several species, including some alleged "glacial relict" types.

CYCLOPOID COPEPODS

Species of cyclopoid copepods, as is well known, have such general distribution, world-wide in some instances, that we need single out here for special mention only two of the sixteen or more species found at Chapel Hill. Others are listed at the end of the paper.

Until this year *Cyclops nanus* Sars, found in weeds on the bottom of White Lake, seems to have been unknown in this hemisphere (Coker, 1938?).

Several years ago, a very small but crassly built copepod identified as *C. crassicaudis* Sars, then known only from Europe, was found in a wheel rut in a wagon road passing through a pine woods *on the top of a hill* just south of the present Kenan Stadium. First collected by L. L. Hill, when a student in our laboratory, it reappeared in the same wheel rut year after year Meantime the species has been recorded from other places in the Western Hemisphere (from New York—Kiefer, 1927; and from Canada—Willey, 1929). Since almost any species of cyclopoid may be expected to be encountered anywhere in the world, the anomaly of the present record derives chiefly from the repeated (up to 1937) and seemingly exclusive local occurrence of this rare species in a temporary water on the very top of a hill; but in Europe also the species

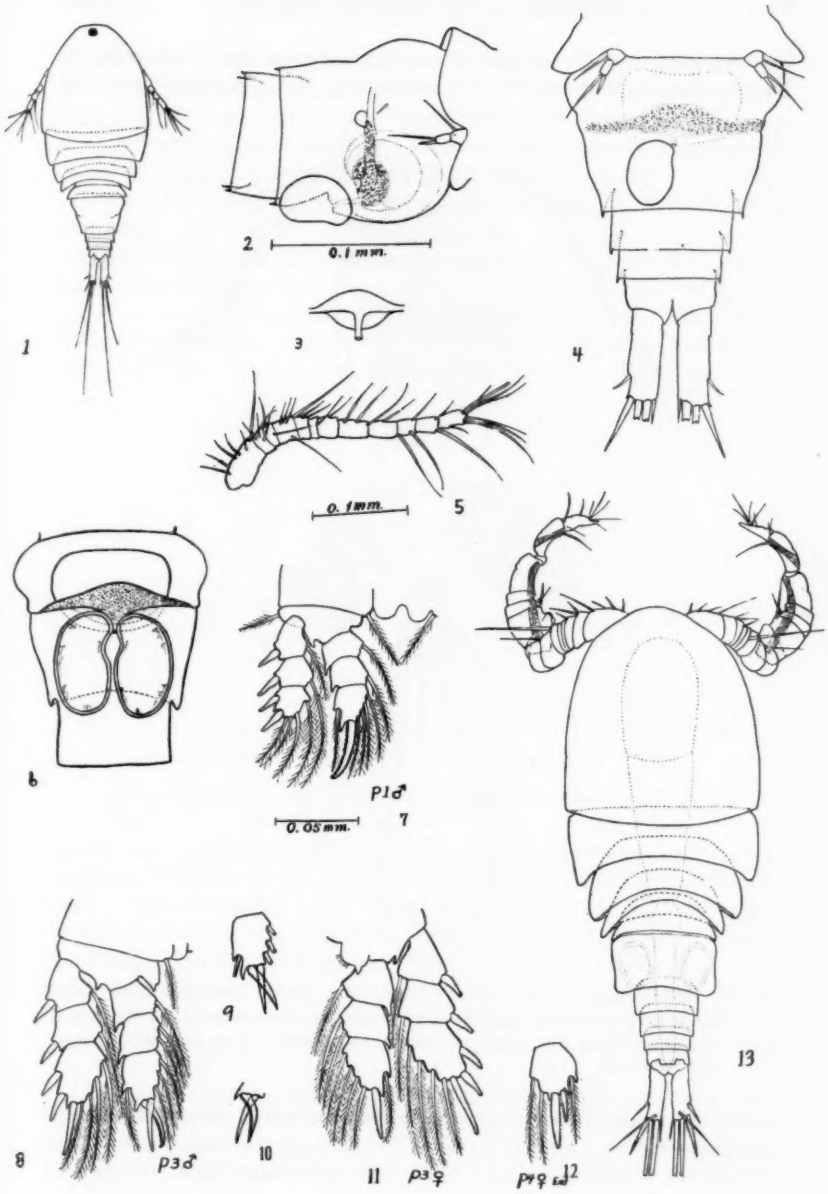
usually occurs in very small temporary waters. As Kiefer has suggested, it is quite possible that the species would be more widely discovered in America if sufficient search were made in the proper sort of places. The identity of *crassicaudis* is not easily mistaken. I know of no other copepod having the peculiarly crossed spines (figs. 9, 10) on the end of the endopod of the fourth foot of the male (Kiefer, 1928, p. 245, Hill and Coker, 1930, p. 216); in what appear to be atypical forms, or subspecies, there is in this place an inner seta and an outer spine (also crossed) (Kiefer, 1928; Gurney, 1933). (Length of our females: 0.58–0.77 mm.)

CLADOCERA

Many species of Cladocera, like some cyclopoid copepods, are seemingly of world-wide distribution, but the aberrant *Holopedium* (of the very small family Holopedidae), with its large gelatinous case and single-branched antennae (of the female) is not one of these. The better known species, *Holopedium gibberum* Zaddach, has been found generally in northern waters relatively free from mineral salts, such as mountain lakes in regions of igneous rock. In Europe its distribution indicates a preference for distinctly acid waters of pH 4.5–6 (Tauson, 1932). In America it has been found in middle northern and northwestern lakes. A related species, *amazonicum* Stingelin, has been described from near the mouth of the Amazon and reported also from Lake Charles, La. I have found no previous record of either species in southeastern states;

FIGS. 1–13. CYCLOPS CRASSICAUDIS G. O. SARS, REGION OF CHAPEL HILL, N. C.

Fig. 1. Dorsal aspect of mature female, contracted, length 0.62 mm.
Fig. 2. Lateral view of genital segments of female, showing spermatophore, seminal receptacle and clear space surrounding it (cf. Fig. 4).
Fig. 3. Seminal receptable (or part of it?).
Fig. 4. Ventral aspect of abdomen, showing one spermatophore, seminal receptacle, clear space surrounding it, deep telescoping of segments, fifth feet (cf. Fig. 2 of same female). Magnification same as for Fig. 2.
Fig. 5. Antenna of female.
Fig. 6. Spermatophores and seminal receptacle.
Fig. 7. First foot of male.
Fig. 8. Third foot of male.
Fig. 9. Terminal segment of endopod of third foot of another male.
Fig. 10. Terminal spines of corresponding segment of a third male.
Fig. 11. Third foot of female.
Fig. 12. Terminal segment of endopodite of fourth foot of female.
Fig. 13. Dorsal aspect of male, length 0.6 mm. (more highly magnified than female).



FIGS. 1–13

but the predominant plankter at certain times in the large pond at Lakeview in the pine lands of Moore County, N. C., is a species of this

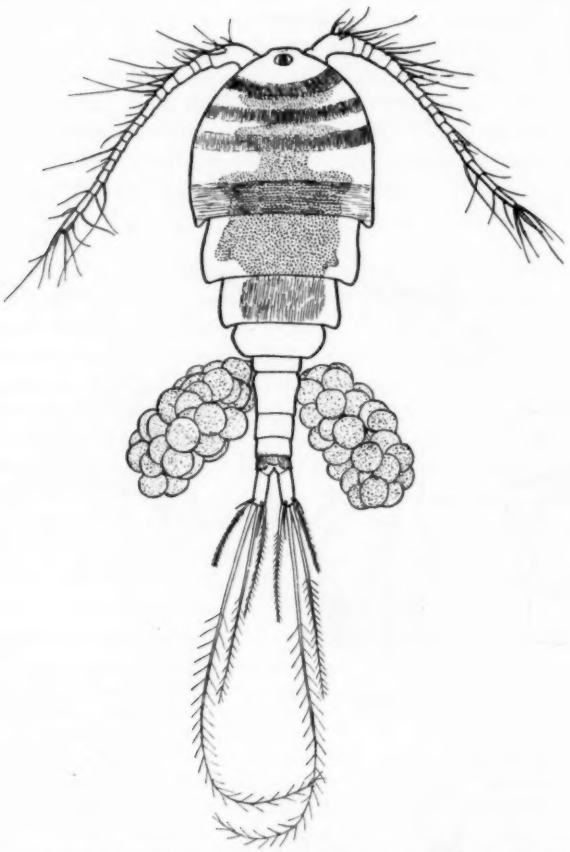


FIG. 14. *Cyclops ater*, female, from Chapel Hill, N. C. The five cross bands shaded with vertical lines were purple in life; the cross band shaded with horizontal lines was blackish purple; the stippled area represents ovary and oviducts.

restricted genus. In spring and early summer a net with 12-inch opening, drawn a couple of hundred feet through the water, would have its 100 cc. bucket more than filled with a virtually pure collection of

Holopedium. Very few are present in the fall. Our species seems closer to *amazonicum* than to *gibberum*.[1] The "lake" is really a large open pond formed forty or more years ago by the damming of a small stream. The water is distinctly but not deeply colored (translucency about 48″) and somewhat acid (pH about 6); the "softness" of the water is further evidenced by the seemingly complete absence of mollusks of any kind.

Besides Cladocera of conventional form with bivalved shell and at least some foliaceous feet, there are on this continent two genera (each with one species) of the naked-bodied Cladocera (Section Gymnomera) with subcylindrical, "prehensile" feet. Hitherto these peculiar Cladocera have been reported only from northern waters. The giant, trans-

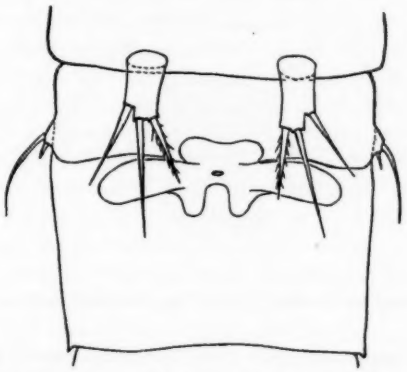


FIG. 15. *Cyclops ater*. Fifth thoracic feet and seminal receptacle

lucent, and rapacious *Leptodora* was recently collected by one of our students, Paul McKee,[2] in a shallow lowland lake some 40 miles from the coast. This is Phelps Lake, Washington County, N. C., embracing 16,600 acres and now a state park. Three examples only were found in a collection taken a little above the bottom where the lake was about 5 feet deep. They seem to pertain to the only known species in the Family Leptodoridae, *Leptodora kindtii* (Focke), but are very small, the largest measuring about 4.9 mm. from brow to tip of anal claws. The

[1] It lacks the teeth on shell and the basal spinule on the caudal spine, characteristic of *gibberum*, and is intermediate between the two known species in number of anal spines (11 or 12).

[2] Mr. McKee's collections were made possible through a grant from the Smith Research Fund.

species may attain a length of 18 mm. in northern lakes. Birge (1918) gives the distribution as "Limnetic in Great Lakes and small lakes in northern United States," but Kofoid (1908, p. 253) reported *L. hyalina* Lilljeborg, presumably the same species, from the expanded Illinois River near Havana, Ill. Through the courtesy of Dr. Waldo L. Schmitt of the U. S. National Museum, I have learned of the finding of *L. kindtii* in the stomachs of fish taken near Conowingo, Md., below the dam on the Susquehanna River. The collections were made by Prof. R. V. Truitt, University of Maryland, who kindly permits this record to be made, and states that *Leptodora* was found abundantly in the stomachs of *Roccus lineatus* in early summer of 1936 and 1937. Dr.

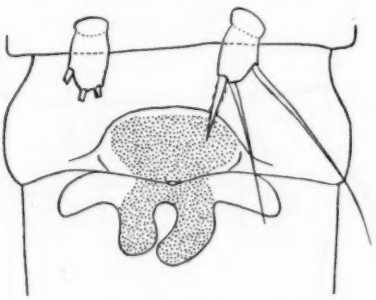


FIG. 16. Same for another individual. Genital plate not showing

Truitt's record seems to have been the southernmost for the genus prior to the present one.

Mr. McKee also obtained, February 13, 1938, from a shallow pond known as Lennon's Millpond in Robeson County near Lumberton, N. C., and some 50 miles from the ocean, a good many examples of *Polyphemus*, presumably *pediculus* (Linné), the sole species of the genus. The surface water was densely populated with algae and covered with duckweed; it contained also a good deal of Utricularia. Birge's statement regarding the distribution of the sole species in the sole American genus in the family is: "Common in Northern United States in lakes, ponds and marshes."

"WATER FAIRIES"

A random dip with a net in a ditch by a newly made road in a swamp just below the old Williams Mill on Cedar Creek near Society Hill, S. C., yielded a single very large and beautifully tinted phyllopod, its trans-

lucent greenish body set off by brilliant red appendages, reddish brown eyes, and a few black pigment spots. Further exhaustive search with dipnet and seine for some hundreds of yards on both sides of the road failed to yield another example. As everyone knows, male phyllopods are much rarer than females. It is noteworthy, therefore, that the single example found here was a male, of the species *Streptocephalus sealii* Ryder, and that it was, according to Dr. E. P. Creaser, the largest known example of the genus, 40 mm. in length with head bent down, or about half again as long as is normal for the species.

SHRIMP

Although *Palaemonetes exilipes* Stimpson, a true shrimp of fresh waters, is widely distributed and reported from about half of the states of the Union (Creaser, 1930, 1932) it seems not to have been recorded in North Carolina except in coastal counties; yet it is a regular inhabitant of the marginal waters at the bathing beach at Lakeview, 100 miles or more from the sea, and, according to a local informant, it occurs plentifully in some other waters not far distant. It is also abundant along shore in White Lake. In the fall of 1933, a dip with a net in a lagoon in a flat swampy woods along New Hope Creek, about 6 miles from Chapel Hill and a little south of the Raleigh road, yielded two examples of this shrimp; the distance from the sea coast is about 130 miles. Further intensive search on this day and succeeding days were entirely fruitless. It is impossible to say whether the two taken were merely strays from an undiscovered local habitat in the region or whether they were recent chance introductions from a distance; such chance introductions must occur or newly formed bodies of water could never become naturally stocked. For more than forty years, at least, collecting has been pursued by graduate students and others in the waters around Chapel Hill with no record of *Palaemonetes*, although the shrimp are large enough (30 mm., more or less, in length) to attract the attention of any collector; but perhaps the lagoons along the New Hope River have not often been visited.[3]

[3] Dr. Waldo L. Schmitt has kindly given me the following records of the U. S. National Museum for *Palaemonetes* from the Carolinas. Of the stations mentioned, only Orangeburg and Summerton, S. C., are remote from the coast.

Salmon Creek, N. C.
Edenton and Newbegun Creek, N. C.
Hales Point, Halifax Co., N. C.
Vicinity of Wilmington, N. C. Fresh water (cypress) pond.
Halifax, N. C.
Lake Mattamuskett, Hyde County, N. C.
Summerton, S. C.
Orangeburg, S. C.

It may be worth while to recall here that the largest specimen of the river shrimp, *Macrobrachium ohionis* (Smith), in the collection of the U. S. National Museum, and perhaps the largest known, was collected by Mr. J. W. Milner in 1878 at Avoca, Bertie County, N. C., at the head of Albemarle Sound, as reported by Dr. Waldo L. Schmitt (1933). Never before or since has the species been recorded from a place as far north in the Atlantic coastal plain.

ANNOTATED LIST OF CYCLOPOID COPEPODS OF THE REGION OF CHAPEL HILL, N. C.

To complete the record of copepods now known in the region of Chapel Hill, a list of the cyclopoids follows. (The locality is Chapel Hill unless otherwise stated.)

1. *Cyclops* (*Macrocyclops*) *ater* Herrick. This large species is always rare, but at Chapel Hill it has been found at several places along Bolin's Creek in quiet water; we record it also from Lakeview and Sweetheart Lake, both near Southern Pines, from White Lake, Bladen County, and from Greenfield Pond near Wilmington. (I have found it also in Quaker Lake in Allegany State Park, N. Y.)
2. *Cyclops* (*Macrocyclops*) *albidus* Jurine. Common in pools.
3. *Cyclops* (*Macrocyclops*) *fuscus* Jurine. Common in pools.
4. *Cyclops* (*Eucyclops*) *serrulatus* Fischer. Common in small waters. A *serrulatus*-like form with extremely long furca ($\frac{FW}{FL} = 0.14$) has been found in a pond in Strowd's Low Ground at Chapel Hill, but only further study, impracticable as yet, would place it as a variant of *serrulatus* or as another species. A form with very short furca ($\frac{FW}{FL} = 0.45$) occurs in bottom fauna of White Lake. The group clearly requires further study.
5. *Cyclops* (*Eucyclops*) *prasinus* Fischer. Common in lakes, including University Lake; found also in a small pond across Bolin's Creek.
6. *Cyclops* (*Paracyclops*) *fimbriatus* Fischer. Not infrequent in marshes.
7. *Cyclops* (*Ectocyclops*) *phaleratus* Koch. Glen Burnie Marsh.
8. *Cyclops* (*Cyclops*) *gigas* Claus (?). A species closely related to *viridis*, taken from the bayou previously mentioned, but now non-existent, was thought by Marsh to be probably *C. magnus*,

described by him from Canada. Kiefer (1929) regards *magnus* as synonymous with the more widely distributed *C. gigas* Claus. Until this group of *viridis* in America has been more thoroughly studied by someone familiar with the European *viridis* we think that all records of the group, including our own, are questionable (see my paper 1934a, p. 271).

9. *Cyclops* (*Cyclops*) *vernalis* Fischer. Very common in several forms commonly called *americanus* (*robustus*), *parcus*, *brevispinosus*.
10. *Cyclops* (*Cyclops*) *bicuspidatus* Claus. Durham City Reservoir.
11. *Cyclops* (*Cyclops*) *venustoides* Coker. In some meadows and spring runs.
12. *Cyclops* (*Cyclops*) *exilis* Coker. In spring runs.
13. *Cyclops* (*Cyclops*) *crassicaudis* Sars. See comment above, p. 77.
14. *Cyclops* (*Cyclops*) *nanus* Sars. White Lake (Coker, 1938?).
15. *Cyclops* (*Cyclops*) *varicans* Sars. Strowd's Low Ground.
16. *Cyclops* (*Cyclops*) *bicolor* Sars. Greenfield Pond, near Wilmington.
17. *Cyclops* (*Orthocyclops*) *modestus* Herrick. Under ice in Bolin's Creek, and at Sparrow's Mill.
18. *Cyclops* (*Mesocyclops*) *leuckarti* Claus. Common in lakes including University Lake.

SUMMARY

1. The calanoid copepods (5 species) collected by the writer in North Carolina, with one exception, were far out of the previously accepted ranges of distribution for the several species.

2. American harpacticoid copepods are too little known for the formulation of distribution records of significance, but two of the nine known species of the region are of a type previously supposed to be distinctly northern, if not a glacial relict, and a third, not now distinguishable from a European species, had been found in this country only in waters of western New York tributary to the Mississippi (see author's paper of 1938). The last mentioned and one of the first two are from White Lake.

3. Records of *Cyclops crassicaudis* in America are extremely rare. Its occurrence at Chapel Hill is very peculiar, but perhaps suggestive as to the kinds of waters in which search for this species should be made everywhere.

4. *Holopedium*, *Leptodora*, and *Polyphemus* are recorded from shallow waters of the coastal plain.

5. The largest *Streptocephalus* of record at the time (and perhaps

still) was collected as a unique specimen (a male) in a newly formed ditch in South Carolina.

6. The range of *Palaemonetes exilipes* Stimpson is extended by records at Lakeview and a unique record at Chapel Hill.

7. Fifteen species of the old broad genus *Cyclops* are definitely identified from the region of Chapel Hill, N. C., besides one from Wilmington, one from White Lake, and one or two others that are not now positively identifiable.

8. The appearance of anomaly in a good many of the records cited probably arises in part from the inadequacy of knowledge of the crustacean fauna of the southeastern United States. The need and the opportunity for studies of fresh-water Crustaceans of the region are clearly indicated.

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CHAPEL HILL, N. C.

PAPERS CITED

BIRGE, E. A.
1918. The water fleas (Cladocera), Chapter 22: 676–740, figs. 1050–1170, *in* Ward and Whipple: Fresh-water biology, New York,

COKER, R. E.
1926. Plankton collections in Lake James, North Carolina: Copepods and Cladocera. Elisha Mitchell Sci. Soc. **41**: 228–258, 11 pls.
1934. Contribution to knowledge of North American fresh-water harpacticoid copepod Crustacea. Ibid. **50**: 75–141, 15 pls.
1934a. Nearly related copepods differentiated physiologically as well as morphologically. Ibid. **49**: 264–284.
1938(?) Notes on the peculiar crustacean fauna of White Lake, North Carolina. (To appear in Arch. Hydrobiol. Stuttgart.)

CREASER, EDWIN P.
1930. The Michigan decapod crustaceans. Papers Mich. Acad. Sci., Arts and Letters **13**: 257–276, figs. 31–40.
1932. The decapod crustaceans of Wisconsin. Trans. Wis. Acad. Sci., Arts and Letters **27**: 321–338, figs. 1–13.

GURNEY, ROBERT
1933. British fresh-water Copepods, Vol. III. London, Ray Society.

HILL, L. L. AND R. E. COKER
1930. Mating habits of Cyclops. Elisha Mitchell Sci. Soc. **45**: 206–220.

KIEFER, FRIEDRICH
1927. Freilebende Süsswasser-Copepoden aus Nordamerika. I. Cyclopiden. Zool. Anz. **72**: 262–268.
1928. Beiträge zur Copepodenkunde (XI). Zool. Anz. **79**: 244–250.
1929. II. *Cyclopoida gnathostoma*. Lfg. 53, Das Tierreich, Crustacea Copepoda. 102 pp., 42 abb.

KOFOID, C. A.
1908. The plankton of the Illinois River, 1894–1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part II. Constituent organisms and their seasonal distribution. Bull. Ill. Lab. Nat. Hist. **8**: 1–361.

MARSH, C. D.
1907. A revision of the North American species of Diaptomus. Trans. Wis. Acad. Sci., Arts and Letters **15**: 381–516, pls. XV–XXVIII.
1933. Synopsis of the calanoid Crustaceans, exclusive of the Diaptomidae, found in fresh and brackish waters, chiefly of North America. Proc. U. S. Nat. Mus. **82**(18): 1–58, 24 pls.

SCHMITT, WALDO L.
1933. Notes on shrimp of the genus *Macrobrachium* found in the United States. Journ. Washington Acad. Sci. **23**: 312–317.

TAUSON, A.
1932. Die Abhängigkeit der Verbreitung von *Holopedium gibberum* Zadd. von einigen Faktoren des äusseren Mediums. Arch. Entw.-Mech. Org. **125**: 770–799, 6 figs.

TURNER, C. H.
1910. Ecological notes on the Cladocera and Copepoda of Augusta, Georgia, with descriptions of new or little known species. Trans. Acad. Sci., St. Louis, Mo. **19**: 151–176, pls. XXXVI–XXXVIII, tables I–V.

WILLEY, A.
1925. Northern Cyclopidae and Canthocamptidae. Proc. Trans. R. Soc. Canada **19**(V): 137–159. Lists *Cyclops bissextilis* n. sp.
1929. Notes on the distribution of free-living Copepoda in Canadian waters. Pt. 2. Some intertidal Harpacticoids from St. Andrews, New Brunswick. Contr. Canad. Biol. (and Fisheries), N. S. **4** (33): 527–539, 30 figs. (*C. bissextilis* = *C. crassicaudis* G. O. Sars).

PLANKTON ROTATORIA FROM NORTH CAROLINA

By Elbert H. Ahlstrom

Plates 6–9

This paper is based upon a rather large group of plankton samples collected in pools, ponds, streams, and lakes in many parts of the state of North Carolina. The three large geographic divisions of the state, the coastal plain, the central piedmont plateau, and the western mountainous region, are all adequately represented. The greatest diversity of forms was found in the material from the coastal region. Material from over a hundred different habitats was examined.

All determinations were made from preserved material, killed by adding Transeau's solution (6 parts water, 3 parts alcohol, 1 part formaldehyde) to collections made with a # 20 bolting silk plankton net. Loricate rotifers are readily identifiable in preserved material; in fact, it is necessary to have most loricate rotifers in a contracted condition to see the distinguishing characters used in their classification. Soft-bodied rotifers are identified with difficulty in preserved material. Their distinguishing features are best seen in expanded living material, and they should be narcotized before killing if their distinguishing characters are to be retained in preserved material. The soft-bodied forms in the North Carolina samples, belonging principally to the notommatid and bdelloid groups, are not adequately treated in this paper. However, such soft-bodied forms were usually few in numbers in the North Carolina samples, being outnumbered several hundred to one by loricate forms in most samples.

Plankton rotatoria in shallow bodies of water are composed largely of adventitious species. There are few truly limnetic species of rotifers. In the discussion that follows no attempt is made to segregate euplanktonts from facultative planktonts or from forms accidentally occurring in the plankton whose usual habitat is the littoral. Any organism taken in plankton samples is considered in this paper as being a plankton organism.

This is the first extensive faunal list of North Carolina rotifers. Rotifers have been intensively studied in the eastern United States

from the following localities: Mt. Desert Island region of Maine (Myers 1931–4), from the Adirondack region of New York (Myers 1937), from Atlantic County in New Jersey (references scattered through many papers of Myers and Harring and Myers), from Washington, D. C. (Harring 1914), and from Florida (Ahlstrom 1934).

The rotatoria found in bodies of water with a pH below 7.0 are quite different from those taken in alkaline habitats. There is a typical alkaline water fauna, having exclusively such genera as *Brachionus*, *Platyias* and *Notholca*; there are many species of other genera that belong definitely to the alkaline fauna alone. Similarly, there is a large number of species whose distribution is limited to acid water associations. Such species are a reliable index to the hardness or softness of a certain body of water. There is a third group of species, tolerant of a rather wide range of pH, which are found in both acid and alkaline habitats. As a rule, loricate rotifers are much more abundant in alkaline fresh waters than in soft water habitats; the number of individuals per unit volume is often many times greater in alkaline habitats than in acid. Acid water habitats, on the other hand, have a much greater diversity of species than hard water associations, and notammatid rotifers are much more common than in hard waters. In North Carolina the bodies of water on the coastal plain are mostly neutral or acid, while the ponds and streams in the piedmont and mountainous regions are commonly hard water associations.

I am deeply indebted to Larry Whitford of the Department of Botany of North Carolina State College, who collected all the samples upon which this paper is based. Mr. Whitford is making an algal survey of the state, in the course of which he has gathered a great number of collections of plankton organisms. He kindly divided many of these samples so that the author could study the rotatorian fauna. I also deeply appreciate the aid given by Frank J. Myers of Ventnor, N. J., during the course of this investigation.

SPECIES OF NORTH CAROLINA PLANKTON ROTATORIA

The number of bdelloid and notommatid rotifers listed is few. The contracted condition of these organisms made their specific determination difficult or impossible. The loricate genera of *Lepadella*, *Colurella*, and *Testudinella* were very widely distributed, and represented by a rather large number of species. Neither *Colurella* nor *Testudinella* is a large genus, so the number of species recorded for the state is noteworthy. Although the list of species for *Lecane* and *Monostyla* are

rather large, yet the number of species of these sizable genera recorded for the state is disappointing; neither genus presents near the diversity of species in North Carolina that it does in Florida or New Jersey. *Brachionus* is not well represented in North Carolina. *Brachionus angularis* and *Brachionus havanaensis* are rather widely distributed, but many common species are rare or absent. *Brachionus calyciflorus* and *Brachionus caudatus* were not recorded at all for the state, though both are very common and widely distributed in alkaline habitats elsewhere in the United States. On the other hand, the alkaline water species, *Platyias patulus*, is widely distributed over North Carolina. Among the Trichocercids, the subgenus *Diurella* was well represented in numbers and species in the state, *Trichocerca rousseleti*, in particular, was very widely distributed and often common in the samples; in the subgenus *Rattulus*, *Trichocerca multicrinis* was often abundant and several other species were common, yet noteworthy by their rarity or absence was the *bicristata-mucosa-cristata-rattus* group of species (a group which is widely distributed in Ohio and elsewhere).

The symbols after specific names have the following significance: A, widely distributed (often common); C, seen in more than ten samples; F, seen in five to ten samples; R, seen in two to four samples; S, seen in but a single collection.

Anuraeopsis fissa (Gosse), A.
Anuraeopsis fissa var. *navicula* (Rousselet), R.
Ascomorpha saltans Bartsch, R.
Asplanchna brightwellii Gosse, R.
Asplanchna priodonta Gosse, F.
Brachionus angularis Gosse, A.
Brachionus budapestinensis Daday, R.
Brachionus havanaensis Rousselet, C.
Brachionus plicatilis Müller, R.
Brachionus quadridentatus Hermann, F.
Brachionus urceolaris Müller, R.
Brachionus zahniseri Ahlstrom, R.
Cephalodella auriculata (Müller), R.
Cephalodella forficula (Ehrenberg), R.
Cephalodella gibba (Ehrenberg), F.
Cephalodella panarista Myers, R.
Cephalodella sterea (Gosse), S.
Chromogaster ovalis (Bergendal), A.
Colurella adriatica Ehrenberg, S.
Colurella bicuspidata (Ehrenberg), A.
Colurella colurus (Ehrenberg), S.
Colurella hindenbergi Steinecke, S.
Colurella mucronulata sp. nov., S.
Colurella obtusa (Gosse), C.
Colurella sulcata (Stenroos), R.
Colurella tesselata (Glasscott), R.
Conochiloides coenobasis Skorikov, R.
Conochiloides dossuarius (Hudson), R.
Conochiloides exiguus sp. nov., S.
Conochiloides natans (Seligo), S.
Conochilus unicornis Rousselet, A.
Dapidia calpidia Myers, S.
Dicranophorus prionacis Harring and Myers, S.
Dissotrocha aculeata (Ehrenberg), F.
Dissotrocha macrostyla (Ehrenberg), A.
Dipleuchlanis propatula (Gosse), R.
Eosphora anthadis Harring and Myers, R.
Euchlanis dilatata Ehrenberg, C.
Euchlanis meneta Myers, F.
Euchlanis parva Rousselet, S.
Euchlanis pellucida Harring, S.

Euchlanis phryne Myers, R.
Euchlanis triquetra Hudson and Gosse, R.
Filina longiseta (Ehrenberg), F (usually abundant when present)
Filina longiseta var. *terminalis* (Plate), R.
Gastropus hytopus (Ehrenberg), C.
Gastropus stylifer Imbof, A.
Kellicottia bostoniensis (Rousselet), A.
Keratella cochlearis (Gosse), A (most common species in state)
Keratella curvicornis (Ehrenberg), F.
Keratella paludosa (Lucks), C.
Keratella serrulata (Ehrenberg), R.
Lecane arcula Harring, F.
Lecane aspasia Myers, R.
Lecane climacois Harring and Myers, F.
Lecane crepida Harring, R.
Lecane curvicornis (Murray), F.
Lecane doryssa Harring, S.
Lecane flexilis (Gosse), C.
Lecane grandis (Murray), S (Brackish Creek, Bayboro)
Lecane hastata (Murray), S.
Lecane hornemanni (Ehrenberg), R.
Lecane leontina (Turner), F.
Lecane ludwigii (Eckstein), R.
Lecane luna (Müller), A.
Lecane luna var. **presumpta** var. nov., R.
Lecane methoria Harring and Myers, S.
Lecane mira (Murray), S.
Lecane nana (Murray), R.
Lecane ohioensis (Herrick), R.
Lecane pertica Harring and Myers, R.
Lecane plesia Myers, S. (Brackish Creek, Bayboro)
Lecane satyrus Harring and Myers, R.
Lecane signifera (Jennings), A.
Lecane stichaea Harring, F. (common Lake Mattamuskeet)
Lecane stokesii (Pell), R.
Lecane tenuiseta Harring, F.
Lecane ungulata (Gosse), C.
Lepadella acuminata (Ehrenberg), A.
Lepadella akrobeles Myers, R.
Lepadella apsicora Myers, R.
Lepadella apsida Harring, R.
Lepadella benjamini Harring, F.
Lepadella cristata (Rousselet), R.
Lepadella cyrtopus Harring, S.
Lepadella dactyliseta (Stenroos), F.
Lepadella latusinus var. *americana* Myers, S.
Lepadella ovalis (Müller), S.
Lepadella patella (Müller), A.
Lepadella quadricarinata (Stenroos), R.
Lepadella quinquecostata (Lucks), F.
Lepadella rhomboides (Gosse), C.
Lepadella salisburii Ahlstrom, S (Lake Waccamaw)
Lepadella triptera Ehrenberg, R.
Lepadella venefica Myers, F.
Lepadella whitfordi sp. nov., R.
Lophocharis salpina Ehrenberg, F.
Macrochaetus collinsii (Gosse), R.
Macrochaetus longipes Myers, S. (Cathernis Lake)
Macrochaetus subquadratus Perty, R.
Monommata grandis Tessin, F.
Monommata longiseta (Müller), F.
Monommata maculata Harring and Myers, R.
Monostyla bifurca Bryce, R.
Monostyla bulla Gosse, A.
Monostyla closterocerca Schmarda, A.
Monostyla cornuta (Müller), C.
Monostyla crenata Harring, A.
Monostyla elachis Harring and Myers, R.
Monostyla furcata Murray, C.
Monostyla hamata Stokes, A.
Monostyla harringi Ahlstrom, S (Brackish Creek, Bayboro)
Monostyla lunaris (Ehrenberg), A.
Monostyla monostyla (Daday), S.
Monostyla obtusa (Murray), R.
Monostyla ornata Harring and Myers, S.
Monostyla perplexa sp. nov., S.
Monostyla quadridentata Ehrenberg, A.
Monostyla stenroosi Meissner, R.
Monostyla tethis Harring and Myers, S.
Monostyla unguitata Fadeev, S.
Monostyla whitfordi sp. nov., S.

Mytilina trigona (Gosse), S (Pond, Morehead City)
Mytilina ventralis (Ehrenberg), R.
Notholca striata (Müller), S.
Notholca striata acuminata (Ehrenberg), S.
Notommata copeus Ehrenberg, F.
Notommata pachyura (Gosse), S.
Pedalia mira (Hudson), C.
Platyias patulus (Müller), A.
Platyias quadricornis (Ehrenberg), R.
Pleurotrocha robusta (Glasscott), R.
Ploesoma formosum Myers, S. (White Lake)
Ploesoma lenticulare Herrick, F.
Ploesoma truncata (Levander), C.
Polyarthra euryptera Wierzejski, A.
Polyarthra trigla Ehrenberg, A.
Pompholyx complanata Gosse, R.
Proales doliaris (Rousselet), R.
Resticula melandocus (Gosse), R.
Rotaria neptunia (Ehrenberg), R.
Scaridium longicaudum (Müller), R.
Squatinella mutica (Ehrenberg), R.
Synchaeta longipes Gosse, F.
Synchaeta pectinata Ehrenberg, A.
Synchaeta stylata Wierzejski, A.
Synchaeta tremula Ehrenberg, S.
Taphrocampa annulosa Gosse, S.
Taphrocampa selenura Gosse, R.
Testudinella angulata Myers, R.
Testudinella caeca (Parsons), R.
Testudinella dentata Myers, S.
Testudinella dicella Myers, R.
Testudinella discoidea sp. nov., R.
Testudinella incisa (Ternetz), C.
Testudinella parva (Ternetz), F.
Testudinella parva var. *bidentata* (Ternetz), R.
Testudinella patina (Hermann), F.
Testudinella reflexa (Gosse), C.
Trichocerca (*Diurella*) *bidens* (Lucks), S.
Trichocerca (*Diurella*) *brachyura* (Gosse), F.
Trichocera (*Diurella*) *collaris* (Rousselet), S.
Trichocerca capucina (Wierzejski), F.
Trichocerca cylindrica (Imhof), C.
Trichocerca (*Diurella*) *edmondsoni* (Myers), S.
Trichocerca elongata (Gosse), S.
Trichocerca (*Diurella*) *insignis* (Herrick), F.
Trichocerca lata (Jennings), S (White Lake)
Trichocerca longiseta (Schrank), F.
Trichocerca mucosa (Stokes), R.
Trichocerca mucripes sp. nov., S.
Trichocerca multicrinis (Kellicott), A.
Trichocerca (*Diurella*) *porcellus* (Gosse), F.
Trichocerca pusillus (Jennings), A.
Trichocerca rosea (Stenroos), R.
Trichocerca (*Diurella*) *rotundata* Myers, F.
Trichocerca (*Diurella*) *rousseleti* (Voigt), A.
Trichocerca scipio (Gosse), F.
Trichocerca (*Diurella*) *similis* (Wierzejski) = *Diurella stylata* Eyferth, A.
Trichocerca stylata (Gosse), S.
Trichocerca (*Diurella*) *sulcata* (Jennings), S.
Trichocerca (*Diurella*) *tenuior* (Gosse), C.
Trichocerca (*Diurella*) *tigris* (Müller), F.
Trichocerca (*Diurella*) *tortuosa* (Myers), S.
Trichocerca (*Diurella*) *weberi* (Jennings), F.
Trichotria spinifera (Western), R.
Trichotria tetractis (Ehrenberg), C.
Trichotria tetractis var. *caudata* (Lucks), R.
Tripleuchlanis plicata (Levander), S (Brackish Creek, Bayboro)

NEW AND UNUSUAL ROTIFERS

Anuraeopsis fissa var. **navicula** (Rousselet)

Anuraeopsis navicula Rousselet, Zool. Jahrb. Syst. **29:** 669, 1910.
Anuraeopsis navicula var. *coelata* de Beauchamp, Linnean Soc. Jour. Zool. **38:** 238, fig. 3, 1932.

The chief distinction between var. *navicula* and *A. fissa vera* is in the pattern of ridges and the tuberculate ornamentation on the lorica of the variety (*A. fissa vera* is but lightly stippled). Supposed differences in the size and shape of the lorica between the two forms breaks down when a series of forms of the two are studied. Even the prominence of ornamentation is a very variable feature in this species, and has been shown to have little or no taxonomic value in the related genus *Brachionus*. I first encountered the variety in material from Parahyba, Brazil, and have since observed it in material from Florida and North Carolina.

Brachionus zahniseri Ahlstrom

Ahlstrom, Trans. Am. Micro. Soc. **53:** 256, pl. 25, fig. 1, 2, 1934.

Observed in several habitats in North Carolina, being very common in freshwater material from Bayboro. It was rare in a sample from a brackish creek at Bayboro in which *Brachionus plicatilis*, a characteristic brackish species, was common. It must therefore be tolerant of highly alkaline situations. Some specimens from North Carolina had the lorica distinctly pustulate.

Colurella hindenburgi Steinecke. Pl. 6, figs. 3, 4.

Steinecke, Schrift. Phys.-ökonom. Ges. Konigsberg i P., Jahrg. **57:** 90, 97, fig. 4, 1916; Hauer, Verhandl. Naturwiss. Vereins in Karlsruhe **31:** 72, figs. 11a–b, 1935.

This small Colurella is closely allied to *Colurella obtusa*. The body is more compressed and the toes are much longer. The toes narrow rapidly, end in long, bristle-like tips, and are rather undulate.

The lorica measures 63μ long, 39μ deep, and 27μ broad. The toes are 27μ long.

Colurella hindenburgi was rare in a freshwater pond at Currituck Sound (May 23, 1937).

Colurella mucronulata sp. nov. Pl. 6, figs. 1, 2.

The lorica is fusiform and greatly compressed from the dorsal view; it is irregularly oval in lateral view, rounded posteriorly, and pointed anteriorly. The lorica is ornamented with a number of longitudinal ridges extending the length of the lorica. The first and second foot joints are relatively short and subsquare, the terminal joint is somewhat longer. The toes are very long; they narrow rapidly to extremely slender, drawn-out tips.

Total length 168μ; length of lorica 109μ, width 38μ, depth 48μ; length of terminal foot joint 12μ; of toes 40μ.

Colurella mucronulata was rare in a mill pond near Pineola (June 18, 1936). It is larger than any described species of Colurella, and is the only species pointed anteriorly. In side view it greatly resembles a Lepadella in the same position. However, in dorsal view it is seen to be a typical Colurella. Its pattern of ornamentation resembles *Colurella sulcata.*

Colurella sulcata (Stenroos). Pl. 6, fig. 5.

Metopidia sulcata Stenroos, Acta Soc. Fauna Flora Fennica **17**: 166, pl. 2, figs. 27–29, 1898.

Colurella sulcata Harring, Bull. U. S. Nat. Mus. **81**: 30, 1913; Fadeev, Proc. Nat. Soc. Kharkov. **50**(1): 9, fig. 9, 1925.

This rugose *Colurella* is apparently widely distributed in the United States in small numbers. It was observed from several localities in North Carolina. The material I have seen of this species differs from the figure of Stenroos in the length of the terminal foot joint: Stenroos' figure shows this to be little longer than the other joints, but in North Carolina material it is twice as long. Fadeev figures this species with a long terminal foot joint.

Length of lorica 78μ, depth 31μ, length of last foot joint 15μ, toes 24μ.

Conochiloides coenobasis Skorikov. Pl. 7, figs. 7, 9.

Skorikov, Arbeiten ichtyolog. lab. Kaspi-Wolg. Fisch.-Ver. Astrachan **3**(5): 30, figs. 1, 2, 1914.

This species is characterized by the ventral antennae arising from a mound-like basal portion nearly as long as the antennae. The stalk-like foot is not particularly long, and on preserved specimens is mostly retracted into the body.

The mastax is of the malleo-ramate type. The right ramus is slightly larger than the left. There are three slender, opposing teeth,

clubbed at their tips, as well as a number of thin, closely crowded accessory teeth in each uncus. Length of trophi 34μ.

This species is closely allied to *Conochiloides natans*. In the latter species the unci formula is $\frac{5+}{5+}$ (length of trophi 42μ) in contrast to $\frac{3+}{3+}$ for *Conochiloides coenobasis*. *Conochiloides natans* is also somewhat larger in size, and has the ventral antennae free for their entire length and not situated on a mound-like basal portion.

Conochiloides coenobasis was observed in Murfreesboro mill pond. I identify the North Carolina specimens with Skorikov's species on the basis of the ventral antennae; Skorikov does not figure or discuss the mastax.

Conochiloides exiguus sp. nov. Pl. 7, figs. 8, 11.

Size small, body pyriform with a long, stalk-like foot, longer than the body length on expanded specimens. Ventral antennae joined for nearly their entire length. The mastax is of the malleo-ramate type. Rami are asymmetric, the right ramus is slightly larger than the left. There are four slender teeth clubbed at their tips in the right incus, as well as a number of closely crowded accessory teeth; the left incus has the last tooth bifurcate, and possesses three other clubbed teeth as well as a number of accessory teeth. Length of trophi 20μ.

Total length of body and stalk-like foot 170-190μ.

Conochiloides exiguus was common in Murfreesboro mill pond. It is closely related to *Conochiloides dossuarius*. It is much smaller than the latter species, however, and has the unci formula of $\frac{1^{+1}+3^{+}}{4+}$ in contrast to the unci formula for *Conochiloides dossuarius* of $\frac{1^{+1}+2^{2+}}{5+}$. The ventral antennae of *Conochiloides exiguus* are joined for even more of their length than are those of *Conochiloides dossuarius*. All individuals noted were solitary. No gelatinous tube was apparent in the preserved material.

Kellicottia, genus novum

Brachionid rotifers with unpaired occipital spines of unequal lengths, one spine being as long as the body proper. Lorica elongated conical, terminating in a long, thin posterior spine. Lorica somewhat compressed dorso-ventrally. Mental margin unornamented, with a shallow median sinus. Body smooth or lightly stippled.

Type species: *Kellicottia longispina* (Kellicott) = *Anuraea longispina* Kellicott = *Notholca longispina* (Kellicott).

Kellicottia longispina (Kellicott)

Anuraea longispina Kellicott, Am. Jour. Micro. Pop. Sci. **4:** 19, fig., 1879.

Anuraea spinosa Imhof, Zool. Anz. **6:** 470, fig. 2, 1883.

Notholca longispina Hudson and Gosse, Rotifera, **2:** 125, pl. 28, fig. 6, 1886.

Occipital spines six: lateral spines subequal and quite long, the left lateral spine somewhat longer than the right; intermediate spines quite short and needle-like; left median spine only slightly longer than intermediate spines, right median spine very long, being nearly half the total length of organism; spines are all very thin and taper to needle-like tips, margin slightly serrate. Mental margin elevated, truncate, with a rather deep U-shaped central sinus. Body proper elongate-conical, though somewhat compressed dorso-ventrally, tapers to a very long and thin posterior spine (slightly shorter than right median occipital spine). Body unornamented save for strengthening ridges arising from base of median spines.

Total length (specimens from Lake Washington near Seattle, Washington) 625μ; length of occipital spines reading from left to right 144–29–42–280–28–118μ; length of posterior spine 224μ, width of body 56μ.

Notholca longispina has not been observed in material from North Carolina, although it undoubtedly occurs. It is a truly limnetic species, found in temperate lakes in all parts of the world. It was originally described from Lake Erie.

Kellicottia bostoniensis (Rousselet). Pl. 9, fig. 1.

Notholca bostoniensis Rousselet, Jour. Quekett Micro. Club, ser. 2, **10:** 337, pl. 21, figs. 1–3, pl. 27, fig. 4, 1908.

Occipital spines four: lateral spines short, recurved near their tips, needle-like; left median spine much longer than right, anterior spines somewhat serrate. Mental margin with a V-shaped central notch dividing the margin into two rounded lobes. Greatest width of body near the center, from which the lorica tapers rapidly to a rather long and thin posterior spine. Body in side view seen to arch dorsally, and both the posterior spine and the long anterior spine are curved ventrally. Short strengthening ridges arise from bases of median

occipital spines. Lorica is ornamented on some individuals with a pattern of longitudinal striations made up of closely placed tubercules; other specimens appear quite smooth.

Total length 364μ; length of anterior spines reading from left to right 26–144–44–24μ; length of posterior spine 118μ; width of body 52μ.

Originally described from Boston, this species seems to be widely distributed in eastern United States, being reported from Florida to New Brunswick (I have seen it in material from Lake Superior). It is widely distributed in North Carolina.

Kellicottia bostoniensis differs from *Kellicottia longispina* in its consistently smaller size; in having four anterior spines rather than six, and in different proportions between the spines; and in the shape of the body.

The genus *Kellicottia* is distinguishable from all other brachionid genera by the character of the occipital spines, which are not paired as is the case in all other genera possessing anterior spines, but are of unequal lengths. All species included in the genus *Notholca* have three pairs of spines, and are bilaterally symmetrical, so that a line drawn through the median bisects the occipital margin into corresponding sets of spines (*Notholca japonica* (Marukawa) = *Pseudonotholca japonica* Marukawa 1928, = *Notholca quadraspinata* Myers 1936 has but two pairs of occipital spines). The occipital margin of *Kellicottia* is never bilaterally symmetrical. No other genus of brachionids has occipital spines of such length as in *Kellicottia*.

The family Brachionidae will include the following genera (some investigators include a number of other genera in this family):

Family Brachionidae
- Subfamily Brachioninae
  - Genus *Brachionus* (including *Schizocerca*)
  - Genus *Platyias*
- Subfamily Anuraeinae
  - Genus *Keratella* (= *Anuraea*)
  - Genus *Notholca* (including *Pseudonotholca*)
  - Genus *Kellicottia*
  - Genus *Anuraeopsis*

Lecane luna var. **presumpta** nov. var. Pl. 7, fig. 1.

The outline of the lorica is very broadly ovate, its greatest width being about four-fifths of the length. The anterior dorsal margin is nearly straight or very slightly convex. The ventral margin has a conspicuous, U-shaped central notch, rounding upwards at the sides.

The dorsal plate is broadly ovate, and somewhat truncate posteriorly; the ventral plate is oval, slightly narrower than the dorsal; it has a transverse fold in front of the foot. The posterior segment is small and rounded; it projects slightly beyond the dorsal plate. The first foot joint is distinct and widest posteriorly, the second truncate pyriform. The toes are about a third of the total length, are parallel-sided, and end in a distinct claw with a small basal spicule.

Total length 165μ; length of dorsal plate 121μ, of ventral plate 128μ; width of dorsal plate 108μ, of ventral plate 103μ, of anterior ventral margin 66μ; length of toe without claw 41μ; claw 11μ.

Lecane luna var. *presumpta* is rather widely distributed; I have seen it in collections from a number of localities in the United States. I am calling attention to this variation by making it a variety. It has characters definitely intermediate between those of *Lecane luna* and *Lecane papuana*. The nearly straight anterior dorsal margin is similar to *Lecane papuana*, as is the anterior sinus in the ventral plate. *Lecane papuana* differs in having two projecting lobes on either side of the central, anterior ventral sinus. *Lecane papuana* is subtropicopolitan in distribution, and has not been found in the United States other than Florida. The record of *Lecane papuana* for Wisconsin by Harring and Myers (1922) is erroneous, and probably refers to the variety. The new variety is proportionately narrower than *Lecane luna*, has the dorsal plate nearly truncate posteriorly, and differs greatly from *Lecane luna* in the character of the anterior margins.

Lepadella akrobeles Myers. Pl. 6, figs. 10, 12.

Myers, Am. Mus. Novitates No. 760, p. 5, figs. 13–15, 1934.

The North Carolina material agrees very closely with Myers' description, except as regards the cross sectional view of the body. There is observable in sectional view not a single rounded dorsal elevation, but three distinct ridges. Observed in material from Lake Mattamuskeet and from a gravel pit pool at Swannanoa.

Lepadella dactyliseta (Stenroos). Pl. 6, fig. 6.

Metopidia dactyliseta Stenroos, Acta Soc. Fauna Flora Fennica **17** (1): 165, pl. 3, fig. 1, 1898.

Lepadella dactyliseta Harring, Proc. U. S. Nat. Mus. **51:** 547, pl. 92, figs. 1–3, 1916; Hauer, Verhandl. Naturwiss. Vereins in Karlsruhe **31:** 88, fig. 19, 1935.

Metopidia rottenburgi Lucks, Rotatorienfauna Westpreuszens, p. 127, fig. 48, 1912.

Total length 112μ; length of lorica 86μ, width of lorica 66μ, depth of ventral head opening 18μ; width at posterior end of foot opening 22μ; length of toes 35μ.

Lepadella dactyliseta is rather widely distributed in North Carolina. The only other American record is from Norfolk, Va. It has apparently been overlooked by other American investigators.

Lepadella quadricarinata (Stenroos). Pl. 6, fig. 13.

Metopidia quadricarinata Stenroos, Acta Soc. Fauna Flora Fennica **17**(1): 165, pl. 3, fig. 2, 1898; Lucks, Rotatorienfauna Westpreuszens, p. 121, fig. 41, 1912.

Lepadella quadricarinata Harring, Bull. U. S. Nat. Mus. **81:** 64, 1913; Hauer, Beiträge Naturkund. Forsch. Sudwestdeutschland **1**(1): 143, pl. 1, figs. 6a–c, 1936.

Harring (1916) in his review of the genus Lepadella considered this as a synonym of *Lepadella patella*. Hauer (1936) considers it distinct. I have noted this species as very common in a collection containing *Lepadella patella* as well, and the two are always sharply separable. *Lepadella quadricarinata* is proportionately wider, and has more prominent and more acute points at the ventral margins of the head opening. The four short dorsal ridges are always developed. The dorsal plate is always somewhat prolonged over the foot opening, and is truncate. The comparative measurements of *Lepadella quadricarinata* and *Lepadella patella* from the same habitat follows:

	L. quadricarinata	*L. patella*
Total length	126μ	105μ
Length lorica	100μ	86μ
Width lorica	80μ	61μ
Width at anterior end	26μ	18μ
Depth foot groove	26μ	24μ
Length terminal foot joint	9μ	7.5μ
Length toes	25μ	22μ

Apparently this species is rather widely distributed.

Lepadella rhomboides (Gosse). Pl. 6, fig. 9.

This widely distributed Lepadellid had a variant in Lake Mattamuskeet in which the toes are much longer than is usual.

Total length 141μ, length of lorica 95μ; width 62μ, width anterior margin 28μ; length of last foot joint 17μ, of toes 35 (–39)μ.

Lepadella whitfordi sp. nov. Pl. 6, figs. 7, 8, 11.

The body is ovoid in outline; the greatest width is slightly anteriorward of the middle of the body; the body terminates posteriorly in a bluntly pointed projection. Four low projections arise near the anterior margin of the dorsum, expand slightly toward the center of the dorsal plate and gradually diminish in width posteriorward; in lateral view the dorsal projections appear as four ridges. The dorsal sinus is moderately deep and broadly U-shaped, the ventral sinus is deeper and broadly V-shaped; the collar is lightly stippled.

The foot groove is narrow, and slightly flaring posteriorly. The foot is relatively short; the terminal joint is longer than the first and second joints, but not so long as their combined length. The toes are very long; they diminish abruptly to extremely slender, drawn-out tips.

Length of lorica 106μ; foot groove 28μ; toes 42 (–47)μ. Width of lorica at widest part 78μ, width at anterior points, 30μ. Depth of ventral sinus 18μ; dorsal sinus 13μ.

Lepadella whitfordi was rather common in a freshwater pond on the beach at Morehead City (June 21, 1937). It was also observed in material from Lake Mattamuskeet, and from a freshwater pond at Currituck Sound. It bears some resemblance to *Lepadella xenica*, but differs in a number of details:

Lepadella xenica	*Lepadella whitfordi*
Shape of lorica distinctly pyriform, widest anteriorly.	Shape ovoid, widest part near middle.
Collar very prominent.	Collar average.
Foot groove suddenly flaring posteriorly.	Foot groove but slightly flaring.
Toes gradually diminishing from base to bristle-like tips.	Toes abruptly diminishing to very long bristle-like tips.
Ventral margins of head opening straight with blunt anterior points.	Ventral margins of head opening convex, with broadly acute divergent points.
Dorsal plate with one ridge.	Dorsal plate with four ridges.

MONOSTYLA Ehrenberg

Edmondson (1935) proposed the inclusion of *Monostyla* in the genus *Lecane* as there have been several species described which are definitely transitional between the genera. *Lecane* has two toes, *Monostyla* only one. Several species have been described in which the toes are partly fused. These are interesting evidences of the derivation of *Monostyla* from a *Lecane*-like ancestor, but they should not invalidate the genus

Monostyla. There are nearly a hundred species of *Lecane* in which the two toes are distinctly separate, and there are at least forty-five valid species in the genus *Monostyla* which always have the two toes completely fused into one. Combining these two large genera under one inclusive genus would obscure the marked differences between two large groups of species, and would gain little. *Lecane* as previously understood is awkwardly large; why overburden it by including at least forty-five more species that can be easily segregated? From both the point of view of utility (which taxonomy must always take into consideration) and in obscuring the natural relationships and differences between large groups of species, the inclusion of *Monostyla* in *Lecane* is very undesirable.

Monostyla ornata Harring and Myers

Harring and Myers, Trans. Wis. Acad. Sci., Arts, and Lett. **22**: 403, pl. 36, figs. 1, 2, 1926.

A few specimens were seen in material from Cathernis Lake (Aug. 12, 1937). This is the second record of this unusually ornamented species for North America.

Monostyla perplexa sp. nov. Pl. 7, fig. 4.

The outline of the lorica is broadly ovate; its width is about two-thirds of the length. The anterior dorsal margin is nearly straight; the ventral margin has a shallow median concavity. No anterior spines are present. The dorsal plate is broadly ovate and somewhat truncate posteriorly. The ventral plate is broadly oval and somewhat narrower than the dorsal plate. The surface markings are limited to a transverse ventral fold a short distance in front of the foot. The lateral sulci are deep. The posterior segment is truncate and rather large, projecting considerably beyond the dorsal plate. The first foot joint is indistinct, the second joint is large and subcircular. The toe is long, nearly one-third of the total length, straight and parallel-sided, terminating in a fairly long claw with two minute, basal spicules.

Total length 120μ; length of dorsal plate 72μ, of ventral plate 79μ; width of dorsal plate 67μ, of ventral plate 63μ; width of anterior margin 51μ; toe without claw 36μ, claw 7μ.

Monostyla perplexa was rather common in Lake Mattamuskeet. It is closely related to *Monostyla lunaris*, but differs in so many details that I am calling it new. It is smaller in size, has quite different anterior margins, is proportionately much wider at the anterior margin,

and differs in various other details of the lorica. The toe is proportionately shorter and does not narrow near the basal spicules as is usually the case in *Monostyla lunaris*.

Monostyla tethis Harring and Myers

Harring and Myers, Trans. Wis. Acad. Sci., Arts, and Lett. **22**: 405, pl. 38, figs. 1, 2, 1926.

A few specimens observed from a fish pond near Pleasant Garden, N. C. Total length 92μ, length ventral plate 69μ, width ventral plate 57μ, width anterior margin 45μ, toe and claw 25μ.

Monostyla unguitata Fadeev. Pl. 7, fig. 5.

Fadeev, Proc. Nat. Soc. Kharkov. **50**(1): 9, fig. 7, 1925.

The outline of the lorica is broadly oval; its width is about four-fifths of the length. The anterior dorsal margin is nearly straight. The ventral margin has a broad, shallow, V-shaped anterior sinus between rather pointed lobes projecting considerably beyond the dorsal plate. The dorsal plate is oval and narrower than the ventral; the ventral plate is more distinctly pyriform than the dorsal and wider; the transverse fold is very strongly marked. The posterior segment is rather small and rounded posteriorly. The first foot joint is indistinct, the second large and subtriangular in form. The toe is fairly long; it is slightly enlarged toward the posterior end; the claws are distinct and quite long. The lorica is ornamented with a pattern of reticular areolations.

Total length 160μ; length of dorsal plate 110μ, of ventral plate 122μ; width of dorsal plate 88μ, of ventral plate 95μ, of anterior margin 58μ; length of toe 30μ, of claw 14μ.

Monostyla unguitata was collected in a canal at Swindell Fork of Lake Mattamuskeet. The North Carolina forms agree fairly well with Fadeev's figures. The Russian forms are proportionately wider and somewhat smaller in size. The shape of the toes and claws and of the anterior margin is very similar in both localities, and are very distinctive. This species is closely allied to *Monostyla cornuta*.

Monostyla whitfordi sp. nov. Pl. 7, figs. 2, 3.

The outline of the lorica is very broadly reversed-ovate; its width is but little less than the length. The anterior margin of the dorsal plate is about straight or slightly convex; the ventral margin is slightly concave; short anterior spines are present. The dorsal plate is very

broadly oval and rounded posteriorly. The ventral plate is much narrower and oval in outline, and is somewhat flexible. The lorica is without surface markings. The posterior segment is large and rounded; it projects with its entire length below the dorsal plate. The coxae plates are fairly large and obtusely rounded posteriorly.

The first foot joint is indistinct, the second joint fairly large and subsquare, projecting slightly beyond the lorica. The toe is fairly long; it is slightly enlarged toward the posterior end; the claw is fairly long, acutely pointed, and has a median dividing line; two basal spicules are present.

Total length 124μ; length of dorsal plate 76μ, of ventral plate 88μ; width of dorsal plate 69μ, of ventral plate 59μ, of anterior margin 50μ; length of toe without claw 36μ, claw 8μ.

Monostyla whitfordi was rather common in a collection from Lake Waccamaw (Aug. 10, 1937). It is related to *Monostyla obtusa* and *Monostyla vastita*. It resembles the latter in the general shape of the body, but the toe is very similar to that of *Monostyla obtusa*. It is readily distinguishable from either of these species. I take pleasure in naming this species for Larry A. Whitford, the collector of all the samples on which this report is based.

Testudinella angulata Myers. Pl. 8, fig. 4.

Myers, Am. Mus. Novitates No. 761, p. 1, figs. 1, 2, 1934.

Seen in material from several North Carolina samples. Total length 133μ; greatest width 88μ; anterior margin 56μ.

Testudinella caeca (Parsons). Pl. 8, figs. 1, 2.

Pterodina caeca Parsons, Jour. Quekett Micro. Club, ser. 2, **4**: 379, pl. 25, fig. 3, 1892; Rousselet, ibid. **7**: 27, pl. 3, fig. 1, 1898.

Testudinella caeca Harring, Bull. U. S. Nat. Mus. **81**: 100, 1913; Carlin-Nilsson, Kungl. Fysiogr. Sallsk. Lund Förh. **5** (Nr. 18): 8, fig. 17, 1935; Hauer, Beiträge zur Naturkund. Forsch. Südwestdeutschland **1**(1): 147, pl. 1, fig. 1a–c, 1936.

Testudinella caeca var. *lermaensis* Ahlstrom, Trans. Am. Micro. Soc. **51**: 249, fig. 6, 1932.

Large examples of this species were found in a freshwater pond on the beach at Morehead City. The anterior dorsal margin has but a small, rounded median elevation, and the lateral antennae are exactly marginal. The foot opening is shield-shaped due to an extension of

the ventral plate overhanging the foot opening as a rudimentary foot sheath.

	Canal, Fairfield	*Cucold Creek, Belhaven*	*Morehead City*
Length	137μ	145μ	170μ
Width	92μ	96μ	112μ
Anterior points	44μ	50μ	57μ

Testudinella dentata Myers. Pl. 8, figs. 6, 7.

Myers, Am. Mus. Novitates No. 761, p. 3, figs. 7, 8, 1934.

Material which is probably referable to this species was collected in freshwater creek, north of Bath. It differs from Myers' description in that the anterior dorsal margin is not notched; the mental margin is more markedly undulate with a wider median sinus; and the body is proportionately much wider. The lorica of the North Carolina form is marked by longitudinal striations, very noticeable along the lateral edges. Total length 127μ; greatest width 102μ.

Testudinella dicella Myers. Pl. 8, fig. 5.

Myers, Am. Mus. Novitates No. 761, p. 5, figs. 11, 12, 1934.

The material I have seen of this species from North Carolina and Florida differs in various details from the figure by Myers. The mental margin has a much narrower median sinus, and the rather flexible dorsal margin has an acutely pointed median spine.

	Rolesville	*Milbournie Pond (Wake Co.)*
Total length	153μ	144μ
Greatest width	75μ	76μ
Anterior points	50μ	56μ

Testudinella discoidea sp. nov. Pl. 8, fig. 3.

The lorica is orbicular in outline. The anterior dorsal is but little elevated if at all, except for a short median spine-like projection. The ventral margin rounds into a rather wide and deep V-shaped central sinus.

The foot opening is wide and shield-shaped in outline; it is terminal or nearly so.

Length of lorica 141μ, width of lorica at widest part 127μ; anterior points 60μ.

Testudinella discoidea was observed in material from Newport and from a ditch with sphagnum near White Lake. I was unable to get

the few specimens seen into position to determine the shape of the transverse section of the body. However, the body is not flexed, is much compressed, and has no ventral ridge. The body is faintly ornamented with longitudinal striations.

Testudinella discoidea is not likely to be confused with any other described species. It resembles *Testudinella caeca* in the shape of the foot opening.

Trichocerca (Diurella) bidens (Lucks). Pl. 9, figs. 8, 9.

Diurella bidens Lucks, Westpr. Botanisch-Zoologischen Verein 1912, p. 66, figs. 12–13; Sachse, Archiv für Hydrobiologie **9**: fig. 3, 1914.
Diurella cavia Fadeev non Gosse, Proc. Nat. Soc. Kharkov **50**(2): 151, pl. 2, fig. 2, 1927.

Harring (1913) considered *Diurella bidens* as a synonym of *Diurella cavia*, and various authors have followed this disposition. However, neither Gosse nor Jennings mentions anterior projections for *D. cavia*: in fact Jennings states, "This species is to be recognized by the very small, plump body, without teeth at the anterior margin of the lorica." *Diurella bidens* has a definite tooth-like projection, quite symmetrically placed, on either side of the head. These cannot be considered mere plaits due to foldings in the head sheath. The head sheath is indistinctly separated from the rest of the lorica, and is provided with several longitudinal plaits at which folding takes place when the head is retracted. The lorica forms an arc on the dorsal side, while the ventral margin is nearly straight. The foot is situated on the ventral surface considerably in front of the posterior end. The two toes are about equal in length.

	Linville, N. C.	(*Lucks*)	(*Fadeev*)
Total length	167μ	170μ	120–150μ
Length toes	50μ	55μ	30– 35μ

Trichocerca (Diurella) edmondsoni Myers. Pl. 9, fig. 2.

Diurella edmondsoni Myers, Am. Mus. Novitates No. 830, p. 14, figs. 10, 12, 1936.

This species is readily distinguished by the prominent, projecting plate on the right side of the head. The material from North Carolina had a very distinct dorsal ridge running from the forward side of the head plate to near the posterior end of the lorica. Myers did not find a ridge on material from New Jersey. The right toe is about two-fifths the length of the longer left toe and is exceptionally stout.

Total length 250μ, length body including foot 143μ, length left toe 110μ, right toe 40μ.

Trichocerca (Diurella) mucripes sp. nov. Pl. 9, fig. 6.

The body is elongate and curved, forming an arc dorsally. The head sheath is distinctly set off from the rest of the lorica, and is marked by a number of longitudinal plaits (probably nine). On the right side the anterior edge bears a prominent tooth. There is an indication of a ridge. The foot is sharply set off from the body, is slender and tapers but little; on the posterior edge is a prominent recurved tooth-like spine. The toes are about equal in length, and about half as long as the body.

Length of body including foot 126μ, length of toes 62μ.

This species was collected sparingly in a fish pond near Pleasant Garden, N. C. It is closely related to *Trichocerca tigris* from which it differs in its smaller size and in the possession of the spine-like process on the foot.

Trichocerca rosea (Stenroos). Pl. 9, fig. 5.

Fadeev, Proc. Nat. Soc. Kharkov. **50**(2): 150, pl. 2, fig. 6, 1925; Hauer, Zool. Anz. **94**: 180, fig. 6, 1931; Ahlstrom 1934, Trans. Am. Micro. Soc. **53**: 265; Edmondson, Trans. Am. Micro. Soc. **55**: 220, 1936; Myers, Am. Mus. Novitates No. 903, p. 6, 1937.

Mastigocerca rosea Stenroos, Acta Soc. Fauna Flora Fennica **17**: 146, pl. 2, fig. 1, 1898.

Rattulus roseus Jennings, Bull. U. S. Fish. Comm. **22**: 341, pl. XV, fig. 137, 1903.

This species has been reported for Florida, Maine, the Adirondack region of New York, and now from North Carolina, and will probably prove to be widely distributed. In material from a canal at Swindell Fork of Lake Mattamuskeet, N. C., the lorica projects backward after the origin of the foot into a definite spine. Specimens measure 290μ long for body including foot, with the main toe 190μ long.

Trichocerca (Diurella) rotundata Myers. Pl. 9, fig. 7.

Myers, Am. Mus. Novitates No. 903, p. 13, figs. 13, 16, 20, 1937.

Rather common in material from North Carolina. Specimens measure 125μ long, with longest toe 40μ long.

Trichocerca stylata (Gosse). Pl. 9, fig. 4.

Harring, Bull. U. S. Nat. Mus. **81:** 105, 1913; Fadeev, Trav. Stat. Biol. du Caucase du Nord **1**(2): 8, figs. 6–8, 1926.

Monocerca stylata Gosse, Ann. Mag. Nat. Hist., ser. 2, **8:** 199, 1851.

Rattulus stylatus Jennings, Bull. U. S. Fish Comm. **22:** 338, pl. 10, figs. 92–94, 1903.

This species appears to be rather widely distributed. I have seen material from Parahyba, Brazil, Lake Xochimilco near Mexico City, as well as Swannanoa, N. C. The head is always thrown into a large number of plaits; the body is plump and somewhat conical-shaped; the main substyle is usually closely appressed along the short toe, so that its length is indeterminable. Jennings (1903) mentions that it might be as long as one-half the length of the main toe; Fadeev (1926) figures it as being about half as long. It is likely that *Diurella inermis* (Lindl.) is a synonym of this species.

Length of lorica and foot 170μ, depth 71μ, toe 52μ.

Trichocerca (Diurella) tortuosa Myers. Pl. 9, fig. 3.

Diurella tortuosa Myers, Am. Mus. Novitates No. 830, p. 15, figs. 14, 17, 1936.

The material from Rockfish, North Carolina, has the lorica but little twisted, and is rather straight on the ventral surface. However, it is obviously referable to this species.

Length body including foot 156μ, length left toe 80μ, right toe 38μ.

LOS ANGELES, CAL.

REFERENCES

AHLSTROM, E. H. 1934. Rotatoria of Florida. Trans. Amer. Micro. Soc. **53:** 251–266.

EDMONDSON, W. T. 1935. Some Rotatoria from Arizona. Trans. Amer. Micro. Soc. **54:** 301–306.

1936. New Rotatoria from New England and New Brunswick. Trans. Amer. Micro. Soc. **55:** 214–222.

HARRING, H. K. 1913. Synopsis of the Rotatoria. Bull. U. S. Nat. Mus. No. 81, 226 pp.

1914. A list of the Rotatoria of Washington and vicinity, with descriptions of a new genus and ten new species. Proc. U. S. Nat. Mus. **46:** 387–405.

1916. A revision of the rotatorian genera *Lepadella* and *Lophocharis* with descriptions of five new species. Proc. U. S. Nat. Mus. **51:** 527–568.

HARRING, H. K., AND MYERS, F. J. 1922. The Rotifer Fauna of Wisconsin. I. A review of the central group of the Notammatids. Trans. Wis. Acad. Sci., Arts, and Lett. **20:** 553–662.

1924. II. A revision of the notommatid rotifers, exclusive of the Dicranophorinae. Trans. Wis. Acad. Sci., Arts, and Lett. **21:** 415–549.

1926. III. A revision of the genera *Lecane* and *Monostyla*. Trans. Wis. Acad. Sci., Arts, and Lett. **22:** 315–423.

1928. IV. The Dicranophorinae. Trans. Wis. Acad. Sci., Arts, and Lett. **23:** 667–808.

HAUER, J. 1924. Zur Kenntnis des Rotatorien-genus *Colurella* Bory de St. Vincent. Zool. Anz. **69:** 177–189.

JENNINGS, H. S. 1900. Rotatoria of the United States, with special reference to those of the Great Lakes. Bull. U. S. Fish Comm. for 1899: 67–104.

1903. A Monograph of the Rattulidae. Bull. U. S. Fish Comm. **22:** 273–352.

MYERS, F. J. 1930. The rotifer fauna of Wisconsin V. The genera Euchlania and Monommata. Trans. Wis. Acad. Sci., Arts, and Lett. **25:** 353–413.

1931. The distribution of Rotifera on Mt. Desert Island (Me.). Am. Mus. Novitates No. 494.

1933A. II. New Notommatidae of the genera *Notommata* and *Proales*. Am. Mus. Novitates No. 659.

1933B. III. New Notommatidae of the genera *Pleurotrocha*, *Lindia*, *Eothina*, *Proalinopsis*, and *Encentrum*. Am. Mus. Nov. No. 660.

1934A. IV. New Notommatidae of the genus *Cephalodella*. Am. Mus. Nov. No. 699.

1934B. V. A new species of Synchaetidae and new species of Asplanchnidae, Trichocercidae, and Brachionidae. Am. Mus. Nov. No. 700.

1934C. VI. New Brachionidae of the genus *Lepadella*. Am. Mus. Nov. No. 760.

1934D. VII. New Testudinellidae of the genus *Testudinella* and a new species of Brachionidae of the genus *Trichotria*. Am. Mus. Nov. No. 761.

1936A. Psammolittoral rotifers of Lenape and Union Lakes, New Jersey. Am. Mus. Nov. No. 830.

1936B. Three new brackish water and one new marine species of Rotatoria. Trans. Amer. Micro. Soc. **55:** 428–432.

1937. Rotifera from the Adirondack region of New York. Am. Mus. Nov. No. 903.

ROUSSELET, C. F. 1908. Note on the Rotatorian fauna of Boston, with description of *Notholca bostoniensis* n. sp. Jour. Quekett Micro. Club, ser. 2, **10:** 335–340.

WHITFORD, L. A. 1936. New and little known Algae from North Carolina. Jour. Elisha Mitchell Sci. Soc. **52:** 93–98.

PLATE 6

Fig. 1. *Colurella mucronulata* sp. nov., lateral view.
Fig. 2. *Colurella mucronulata* sp. nov., ventral view.
Fig. 3. *Colurella hindenburgi* Steinecke, lateral view.

Fig. 4. *Colurella hindenburgi* Steinecke, dorsal view.
Fig. 5. *Colurella sulcata* (Stenroos), lateral view.
Fig. 6. *Lepadella dactyliseta* (Stenroos), ventral view.
Fig. 7. *Lepadella whitfordi* sp. nov., ventral view.
Fig. 8. *Lepadella whitfordi* sp. nov., dorsal view.
Fig. 9. *Lepadella rhomboides* (Gosse), dorsal view.
Fig. 10. *Lepadella akrobeles* Myers, dorsal view.
Fig. 11. *Lepadella whitfordi* sp. nov., cross section of body.
Fig. 12. *Lepadella akrobeles* Myers, cross section of body.
Fig. 13. *Lepadella quadricarinata* (Stenroos), dorsal view.

PLATE 7

Fig. 1. *Lecane luna* var. *presumpta* nov. var., ventral view.
Fig. 2. *Monostyla whitfordi* sp. nov., dorsal view.
Fig. 3. *Monostyla whitfordi* sp. nov., ventral view.
Fig. 4. *Monostyla perplexa* sp. nov., ventral view.
Fig. 5. *Monostyla unguitata* Fadeev, ventral view.
Fig. 6. *Monostyla cornuta* (Müller), ventral view.
Fig. 7. *Conochiloides coenobasis* Skorikov, lateral view.
Fig. 8. *Conochiloides exiguus* sp. nov., lateral view; specimen partly contracted.
Fig. 9. *Conochiloides coenobasis* Skorikov, trophi.
Fig. 10. *Conochiloides natans* (Seligo), trophi.
Fig. 11. *Conochiloides exiguus* sp. nov., trophi.
Fig. 12. *Conochiloides dossuarius* (Hudson), trophi (based upon a sketch furnished by Frank J. Myers).

PLATE 8

Fig. 1. *Testudinella caeca* (Parsons), ventral view, specimen from Cucold Creek, Belhaven.
Fig. 2. *Testudinella caeca* (Parsons), ventral view, specimen from pool at Morehead City.
Fig. 3. *Testudinella discoidea* sp. nov., ventral view.
Fig. 4. *Testudinella angulata* Myers, ventral view.
Fig. 5. *Testudinella dicella* Myers, ventral view.
Fig. 6. *Testudinella dentata* Myers, ventral view.
Fig. 7. *Testudinella dentata* Myers, lateral view.
Fig. 8. *Testudinella parva* (Ternetz), ventral view.
Fig. 9. *Testudinella incisa* (Ternetz), ventral view.
Fig. 10. *Testudinella reflexa* (Gosse), ventral view.
Fig. 11. *Testudinella parva* var. *bidentata* (Ternetz), ventral view.

PLATE 9

Fig. 1. *Kellicottia bostoniensis* (Rousselet), dorsal view.
Fig. 2. *Trichocerca edmondsoni* Myers, lateral view.
Fig. 3. *Trichocerca tortuosa* Myers, lateral view.
Fig. 4. *Trichocerca stylata* (Gosse), lateral view.

Fig. 5. *Trichocerca rosea* (Stenroos), lateral view.
Fig. 6. *Trichocerca mucripes* sp. nov., lateral view.
Fig. 7. *Trichocerca rotundata* Myers, lateral view.
Fig. 8. *Trichocerca bidens* (Lucks), lateral view.
Fig. 9. *Trichocerca bidens* (Lucks), view of head sheath from above.

PLATE 6

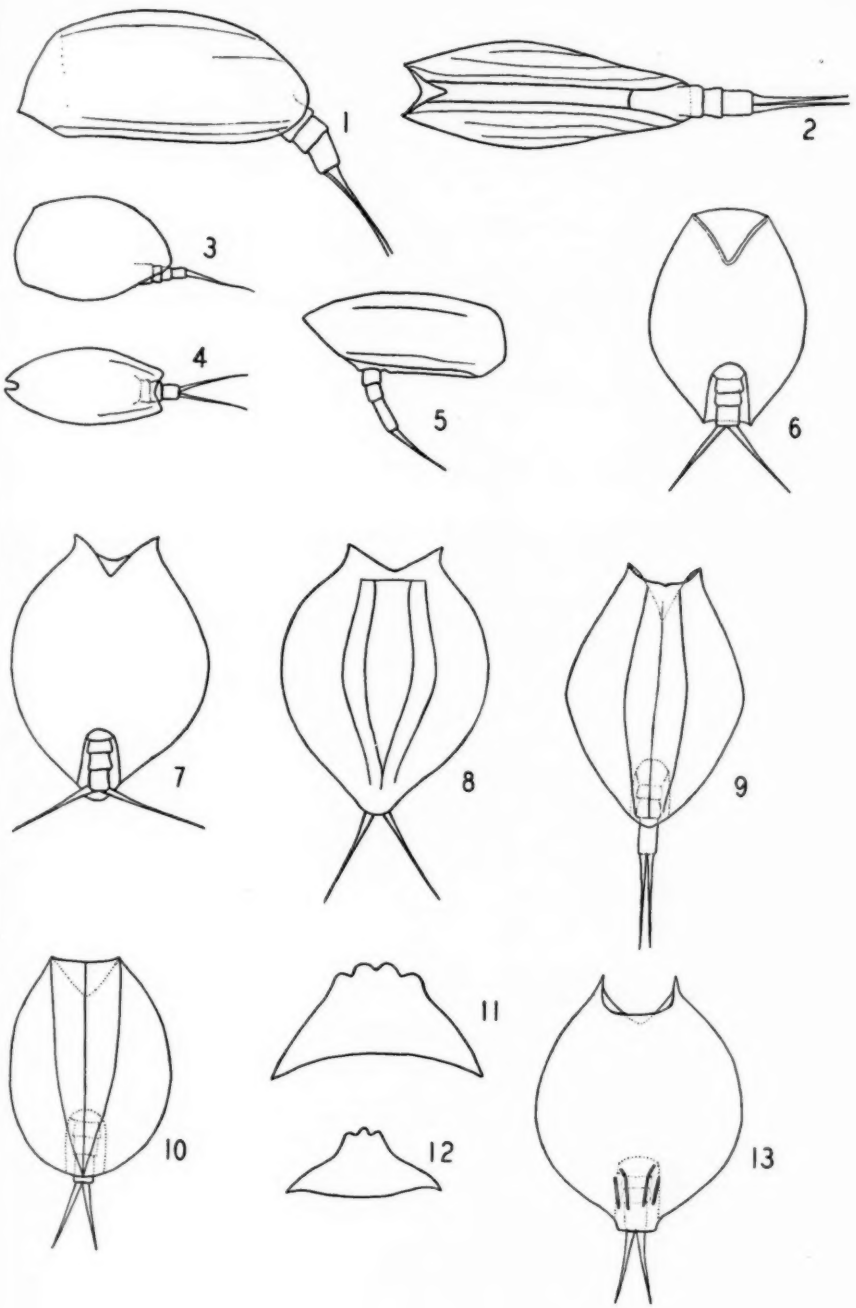

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PLATE 7

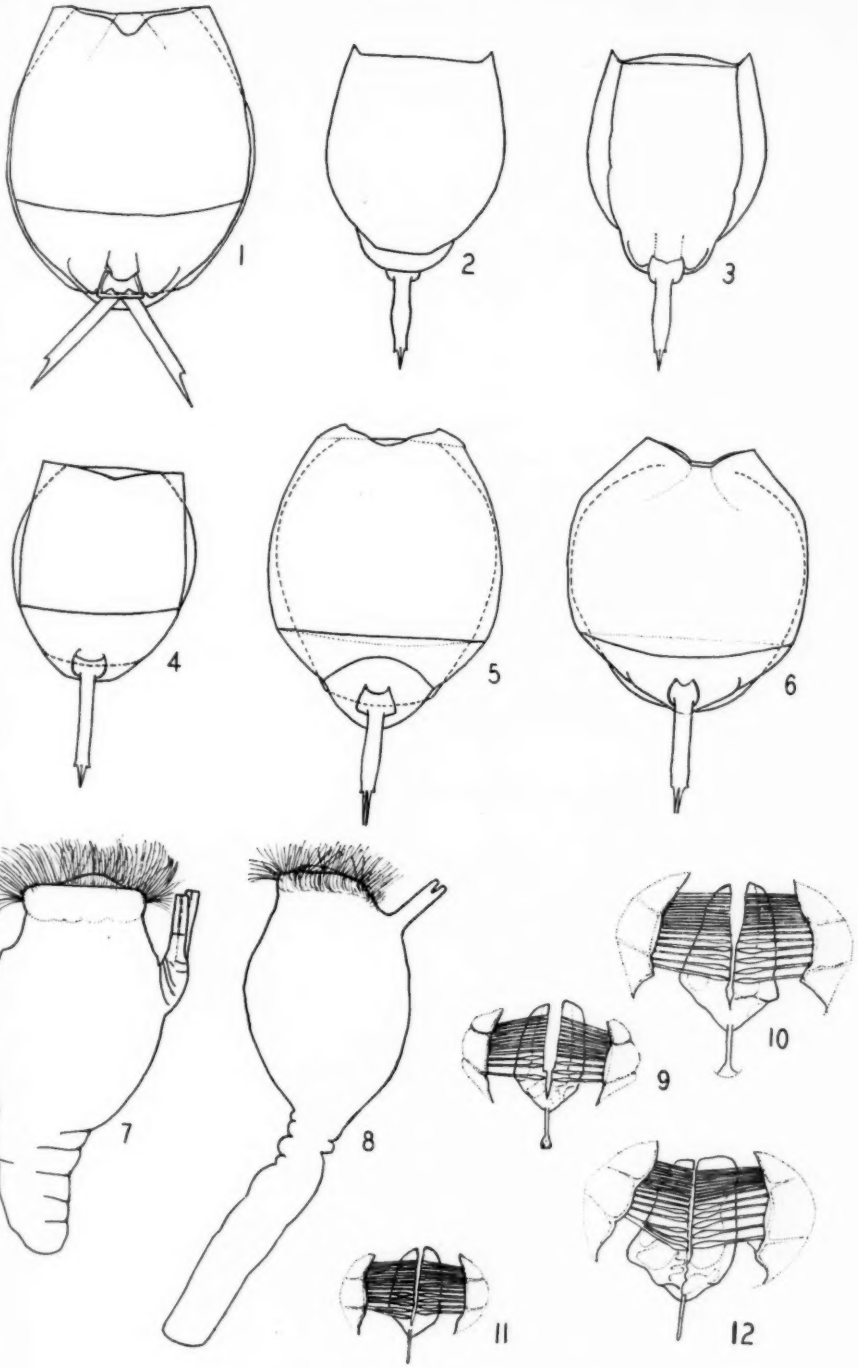

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PLATE 8

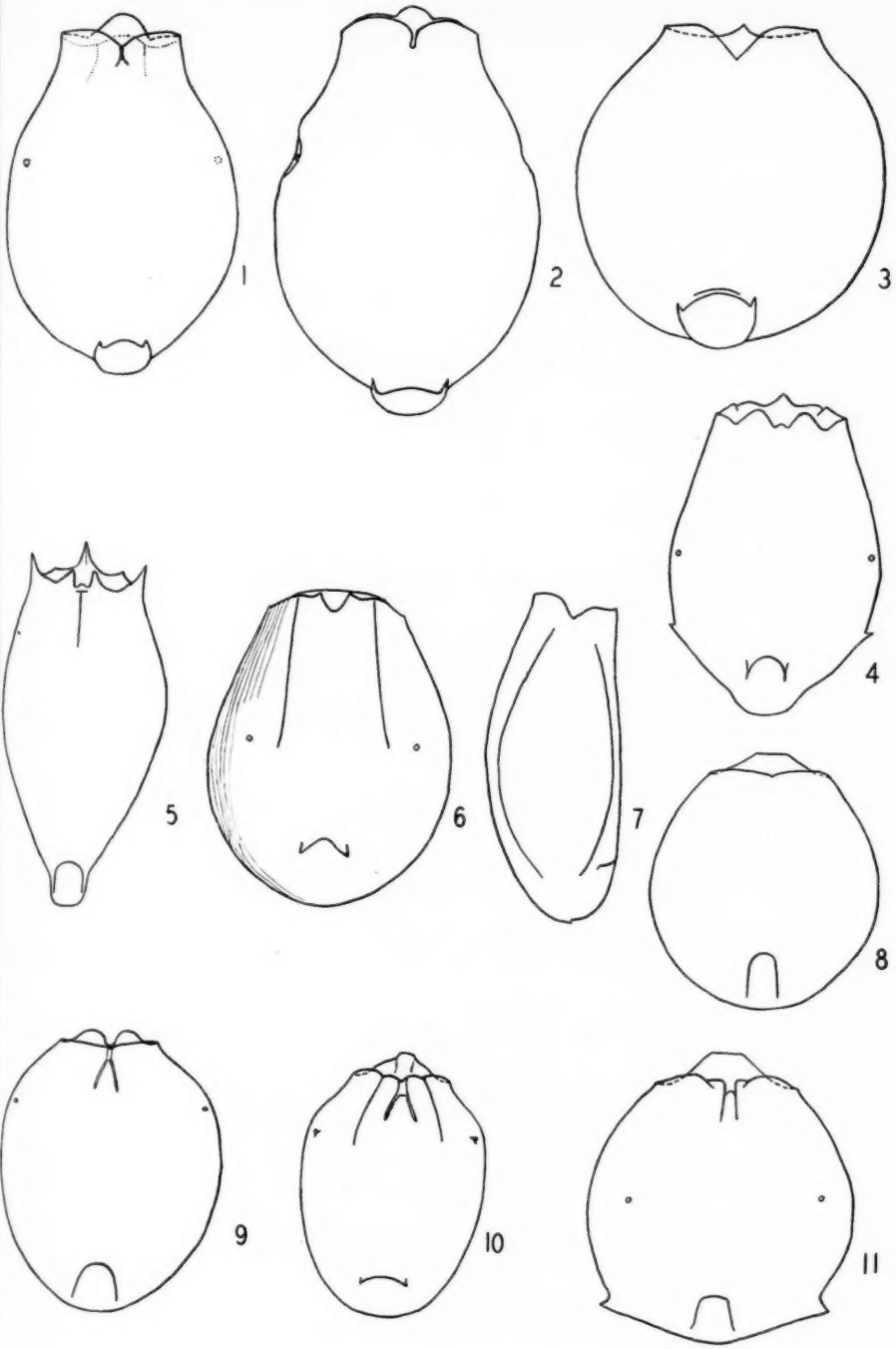

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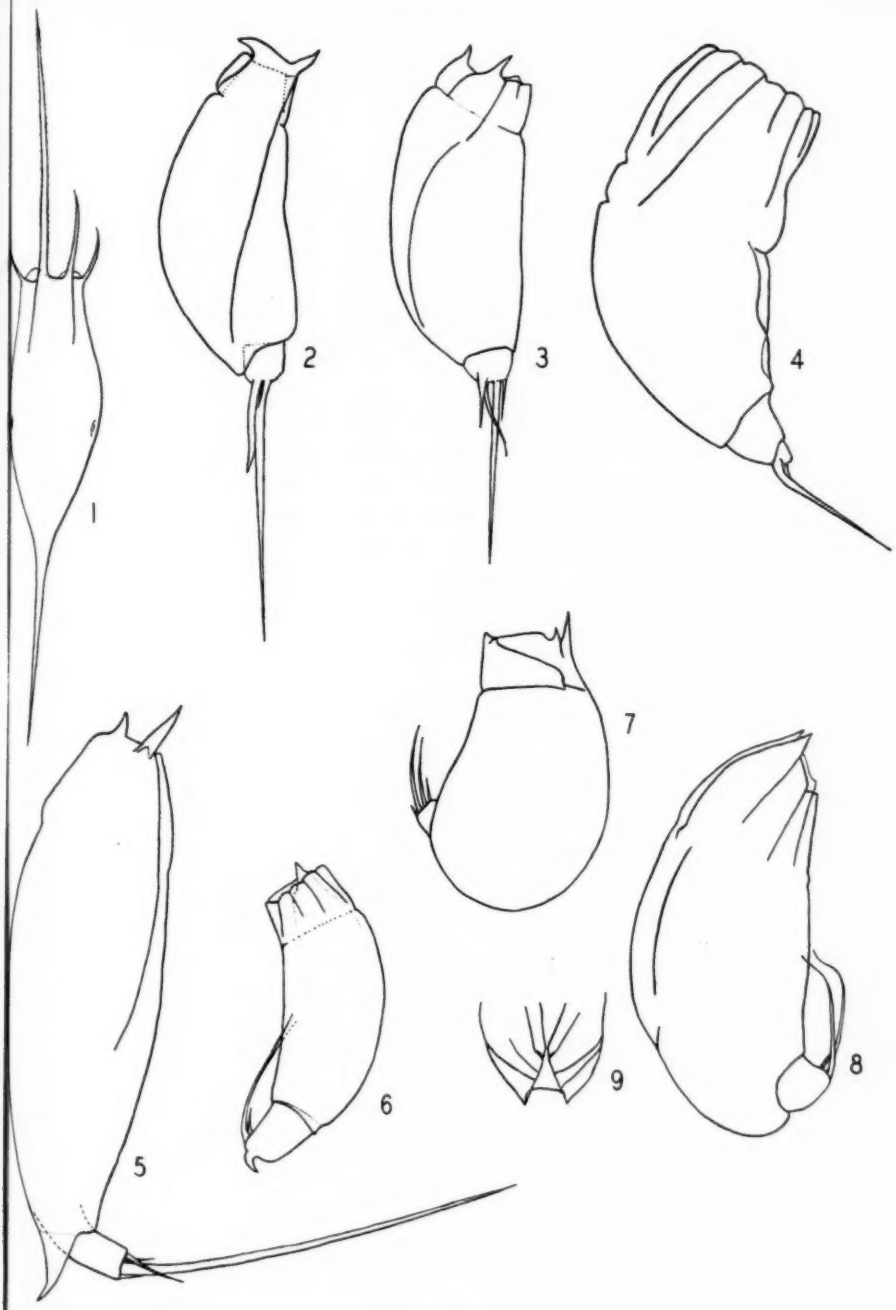
PLATE 9



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STRUCTURE AND DIVISION IN THE ASTOMATOUS CILIATE METARADIOPHRYA ASYMMETRICA N. SP.

By C. Dale Beers

Plates 10 and 11

INTRODUCTION

The genus *Metaradiophrya* was established by Heidenreich (1935) to receive two well-known species of *Hoplitophrya* Stein, 1860, which differ significantly from other members of the genus. These are *H. lumbrici*, which was described originally as *Opalina lumbrici* by Dujardin (1841), and *H. falcifera* Stein, 1861. As a result of this division, *Hoplitophrya* now embraces slender, elongate, astomatous infusoria which have dorsally a single longitudinal row of from 15 to 30 contractile vacuoles and ventrally in the mid-line a single spicule bearing at its anterior end a small, pointed tooth; whereas *Metaradiophrya* embraces shorter and broader astomatous forms which have laterally two rows of a few contractile vacuoles each and anteriorly for attachment a hook with which is associated a system of ectoplasmic supporting fibers. Both genera inhabit the alimentary tract of oligochaetes.

Reference may be made to the studies of Cheissin (1930) and Heidenreich (1935) for details of classification in the group Astomata. Their work has done much to alleviate the taxonomic confusion occasioned by the inadequate descriptions of earlier investigators, as well as by the absence in these ciliates of a mouth and associated feeding organelles—structures of primary importance in the classification of infusoria. It will suffice to state that Cheissin (1930, p. 605) united in the Hoplitophryidae all Astomata that possess conspicuously differentiated skeletal elements, whether in the form of a hook-like organ of attachment or a system of supporting fibers or both, and that Heidenreich recognizes in the Hoplitophryidae eight genera, one of which is *Metaradiophrya*. Heidenreich (p. 335 and p. 338) gives the complete synonymy of *M. lumbrici* and *M. falcifera*.

Since the specimens of *Metaradiophrya* that I have found in the intestine of the earthworm *Eisenia lönnbergi* do not agree with the descriptions of either of the two known species as regards the arrange-

ment of the skeletal elements and the structure of the micronucleus, I shall designate them as *Metaradiophrya asymmetrica* n. sp., because of the asymmetrical arrangement of the skeletal elements. Unfortunately, I have had no opportunity to examine specimens of *lumbrici* and *falcifera*.

SOURCE OF MATERIAL; METHODS; INCIDENCE OF INFECTION

The worms from which the ciliates were taken agree with Smith's description (1917, p. 164) of *Helodrilus* (*Eisenia*) *lönnbergi* (Michaelsen) as regards all important diagnostic features except the position of the first dorsal pore. According to Smith, it is found in intersegmental groove 7/8; in the specimens that I have examined it occurs in 4/5, but this difference is no doubt one of subspecific import. Stephenson (1930, p. 908) calls attention to the inconvenience of designating the common Lumbricids by generic, subgeneric and specific names and considers the subgenera under *Helodrilus* as independent genera. Following his practice, I am designating the host as *Eisenia lönnbergi*.

To obtain ciliates for study, the worms were narcotized in 1% chloretone in 10% alcohol, rinsed thoroughly under the tap and rolled on filter paper to remove the excess water. Next, they were opened by a longitudinal incision in the body wall and were pinned out on sheet cork. Finally, the intestine was opened and portions of the contents were removed by means of a small wooden spatula to large drops of distilled water in depression slides. From these the ciliates were transferred to micro slides by means of a small pipette. Dilution of the intestinal contents with distilled water was much less harmful to the ciliates than dilution with any of a number of inorganic salt solutions that were tried.

Permanent whole mounts were made by attaching fixed specimens to slides with celloidin before staining (Aunap, 1927). Sections were prepared by transferring the fixed specimens to a small bag made of cat mesentery (Beers, 1937).

The immersion of the hosts in chloretone had no observably injurious effect on the ciliates, for specimens removed from active worms lived no longer outside their host than those from narcotized worms, nor did the two groups differ in shape, structure or behavior. Early attempts to remove the ciliates from normal, active worms proved unsatisfactory and exasperating, since such worms, when pinned out, invariably tore themselves into contracted fragments. This practice was discontinued as soon as the relative harmlessness of the chloretone procedure was established, though special precautions—the rinsing and drying treatment already mentioned—were taken to prevent either the chloretone or tap water from coming in contact with the ciliates.

Unfortunately, I have found as yet no medium in which *Metaradiophrya* will live for any appreciable length of time outside of its host. Indeed, it proved to be somewhat difficult to ascertain, with the desired degree of accuracy, the normal dimensions of the ciliate—the dorsoventral one in particular—for the animals swell rapidly after removal from their host. I hesitate to attribute this to oxygen toxicity—the usual explanation—until the probable chemical and physical inadequacies of the media have been evaluated. Specimens examined in coelomic fluid of the earthworm showed least swelling and lived longest. Further attempts are in progress to determine the cultural needs of the ciliates.

More than 400 adult specimens of *Eisenia lönnbergi* from the environs of Chapel Hill were examined for *Metaradiophrya*. Approximately 60% of them were infected, but not heavily. As a rule, only five to ten ciliates could be found in an infected host. Undoubtedly some were overlooked, for most of them seemed to be closely applied to the lining epithelium of the intestine. Often when the contents appeared to be negative or to contain only a ciliate or two, the examination of scrapings from the intestinal lining showed numbers to be present. Six worms were exceptions, in that each contained at least 150 specimens; these six hosts furnished nearly all of the division stages that were found. If the intestine is thought of as consisting of three parts, fully 90% of the specimens of *Metaradiophrya* were found in the middle third, with the remaining few in the posterior part of the anterior third. Neither conjugation nor encystment was observed. I can offer no satisfactory comment on the method of transmission from host to host.

It may be mentioned at this point that of the 400 worms examined, fully 80% were infected with another intestinal ciliate, a species of *Hysterocineta* Diesing, 1866, which is probably known better under the synonym *Ladopsis* Cheissin, 1928. This form, like its near relative, *Ptychostomum*, is remarkable in having the mouth at the extreme posterior end of the body. A study of its structure and division is now in progress. Approximately 50% of the 400 worms harbored both *Metaradiophrya* and *Hysterocineta*, but the two ciliates were rarely found in the same region of the intestine. In general, *Hysterocineta* occupied a region posterior to that inhabited by *Metaradiophrya*.

A further point concerning the occurrence of the two ciliates is of interest. A species of the earthworm *Pheretima* measuring up to 20 cm. in length was always found along with the specimens of *Eisenia*. Yet the examination of 110 specimens of *Pheretima* failed to disclose a single ciliate. Whether this indicates a high degree of host specificity

in the ciliates or results merely from the inability of the infective stages to pass unharmed through the more powerful gizzard of *Pheretima* is not clear.

METARADIOPHRYA ASYMMETRICA N. SP.; DESCRIPTION; COMPARISONS WITH M. LUMBRICI AND M. FALCIFERA

Shape and size. The shape of *Metaradiophrya asymmetrica* permits for descriptive purposes the use of the topographic terms usually applied to bilaterally symmetrical animals. Dorsal and ventral surfaces are clearly differentiated. The dorsal surface is somewhat convex and the ventral surface, on which is found a hook for attachment to the intestinal epithelium, is in general flattened or slightly concave (figs. 2 and 3). The animal as a whole is dorso-ventrally flattened, but its dorso-ventral dimensions vary in different regions of the body. It is thinnest at the posterior end (figs. 2, 3, and 12) and increases in thickness as the anterior end is approached until the region of the attachment organelle is reached; here there is a rather sudden decrease in thickness to produce on the antero-ventral surface an excavation or depression (fig. 2, D) along the right margin of which lies the shaft (S) of the hook (H). The anterior end of the cell body is rounded, while the posterior end is either rounded or, more commonly, truncated. Often the truncation is oblique, so that the right lateral margin is slightly longer than the left (fig. 1, *ventral* view of adult individual). The cell body is non-contractile and but slightly flexible. Adult specimens measure 115–150μ in length and 55–70μ in width.

A relatively thin layer of hyaline ectoplasm is clearly differentiated from an inner region of finely granular endoplasm (figs. 2 and 4, the latter a cross section).

In size *M. asymmetrica* shows no significant differences from *M. lumbrici* and *M. falcifera*. Cépède (1910, p. 401) reports that *Hoplitophrya hamata* Cépède (= *M. lumbrici*) from *Lumbricus terrestris* and *L. rubellus* measures 135μ by 66μ and Heidenreich's specimens (p. 338) from *L. rubellus* and *Eisenia foetida* measure 120–140μ by 60–70μ. According to Cépède (p. 405), the largest specimens of *Hoplitophrya falcifera* (= *M. falcifera*) measure 125μ by 85μ, whereas those found by Heidenreich (p. 338) in *L. terrestris* measure 120–150μ by 70–90μ.

The three species are also in close agreement regarding the general shape of the cell body. They are all flattened dorso-ventrally and have rounded anterior borders. The posterior border of *lumbrici* is truncated (Cépède, p. 400) as in *asymmetrica*, though it is more rounded in *falcifera*, so that the general cell outline is oval or elliptical (Cépède, p. 405).

Cépède in his description of *lumbrici* (p. 400 and p. 557) makes no mention of an antero-ventral depression; presumably it is present. However, he describes and figures a depression in *falcifera* (p. 407 and Pl. 9, fig. 2) and regards it as having a suctorial function. In *asymmetrica* I have been quite unable to adduce any evidence indicating that this region functions as a sucker. It shows no marginal ectoplasmic thickening (fig. 4) such as would be expected were its function suctorial and it is everywhere provided with cilia which would surely interfere seriously with any suctorial action.

Macronucleus: A slender, cylindrical macronucleus lies in the midline of the body (fig. 1). In general, it is straight, though in some specimens it shows wide undulations in the sagittal plane (fig. 2). In adult specimens it is at least 100μ long and 5–7μ in diameter. With nuclear dyes it shows a lightly staining matrix in which are embedded irregular, closely packed, deeply staining chromatin granules (fig. 15). The macronuclei of *lumbrici* and *falcifera* are of this same type and have been described and figured by Stein (1854, 1861) and Cépède.

Micronucleus: The single micronucleus is vesicular and has a diameter of 3.5–5μ. It is found always well to the right of the macronucleus and just within the posterior half of the cytoplasm (fig. 1). It contains a single, spherical, central karyosome which stains intensely with haematoxylin or acid fuchsin and has a diameter of 2–2.5μ. Clearly the karyosome contains all of the chromatin, for between it and the nuclear membrane there is only a clear space about 1μ across. In well stained preparations the micronucleus is quite conspicuous.

This type of micronucleus is very different from that described in *lumbrici* and *falcifera*. In *lumbrici*, according to Cépède (p. 403), it is a small fusiform body measuring only 5μ by 1.3μ. His figure (Pl. 11, fig. 26) shows it as a very inconspicuous structure quite near the ectoplasm of the left side of the cell. In *falcifera*, according to Stein (1861) and Cépède (p. 407), the micronucleus is likewise a small ovoidal body. Neither Cépède (Pl. 9, fig. 3 of *falcifera*) nor Stein (1854, Pl. 5, fig. 24 of *lumbrici*) shows the micronucleus in figures of dividing specimens. Evidently it is an inconspicuous structure in these two species.

Skeletal elements: Undoubtedly the skeletal elements are the structures of greatest interest in *M. asymmetrica*. They consist of a rigid, hook-like organelle of attachment, which is probably chitinous, and of a system of supporting fibers. The attachment organelle consists of a slightly bent shaft which is firmly embedded in the ectoplasm of the antero-dextral margin of the cell body (figs. 1 and 2, S) and is continued anteriorly as a short, stout, sharply pointed hook (H). The hook lies

in the mid-ventral line with its apex directed ventro-posteriorly. I have been quite unable to identify either in the living animal or in stained whole mounts and sections any myonemes for moving the hook. Neither have I been able to observe in living specimens any movement of the hook or any evidence of an articulation between hook and shaft. The shaft is about 30μ long and 2μ in diameter; the hook is about 10μ long.

The supporting fibers ("Skelettstrahlen") are found in the ectoplasm of the ventral surface (fig. 1, F and TF). In general, their course is longitudinal and they are restricted to the depressed antero-ventral surface. They lie just beneath the longitudinal rows of cilia and parallel to them. In living specimens they may be mistaken easily for continuations of the ciliary rows. Only in suitably stained preparations can their size, arrangement and extent be clearly ascertained. With iron haematoxylin following Schaudinn or Bouin fixation they stain intensely black, as do the hook and shaft. With Mallory's stain these structures are colored a brilliant red, whereas they scarcely stain at all in Delafield's haematoxylin.

The fibers do not have a bilaterally symmetrical arrangement. Those of the left half of the antero-ventral surface (fig. 1, F) arise in the mid-line near the base of the hook and diverge slightly in passing sinistro-posteriorly. The fibers lying to the right of the mid-line originate near the shaft and continue directly backward. There are from 25 to 30 fibers in this entire group. They are spaced at intervals of 1μ and they become progressively shorter from left to right across the depression. All of them originate dorsal to the shaft. The longest ones measure 40μ in length, the shortest ones about 7μ. Proceeding toward the right, there follows an area embracing six to eight rows of cilia that is quite devoid of fibers (fig. 1, AF). Finally, there is a tuft of from seven to nine fibers along the right margin of the depression (fig. 1, TF). These originate near the end of the shaft and, diverging slightly, continue posteriorly for 5–10μ.

The superficial position of the fibers and their appearance when viewed transversely are shown in fig. 4 (section of a specimen in which the macronucleus extended farther forward than in fig. 1; through the larger group of fibers). The fibers (F) are elliptical or oval in cross section. They lie in the ectoplasm (EC) very near the external surface, as does the shaft (S) of the hook also. Basal granules cannot be identified with certainty in my sections of the fibers, though cilia are invariably present in this region. Evidently the fibers lie directly beneath

the rows of granules and so near them that the two systems cannot be differentiated. Similar fibers in *Radiophrya tubificis* are likewise oval in cross section and parallel to the ciliary rows, but they lie at the side of the rows, not directly beneath them, according to Rossolimo and Perzewa (1929). The fibers of *Metaradiophrya* no doubt give rigidity to the anterior end of the organism and are therefore to be looked on as supporting elements.

A consideration of the arrangement of skeletal elements in the related genus *Radiophrya* is appropriate at this point. In *Radiophrya*, according to Rossolimo (1926), they consist essentially of a bilaterally symmetrical V-shaped piece ("Pfeilspitze"), the apex of which lies anteriorly in the mid-line and points forward, and of a number of supporting fibers which begin in the V-piece and continue backward in the ectoplasm of the ventral surface. In *R. prolifera* from the oligochaete *Styloscolex baikalensis* and in *R. tubificis* from *Tubifex tubifex* the skeletal elements are of the foregoing type and evidently lend rigidity to the anterior end (Rossolimo, 1926; Rossolimo and Perzewa, 1929), whereas in *R. hoplites* a tooth is articulated with the apex of the V-piece (Rossolimo, 1926; Cheissin, 1930, p. 560). Heidenreich, correctly it would seem, regards this arrangement as the underlying plan from which the skeletal elements of *Metaradiophrya* may be readily derived. His observations on *falcifera* show that a V-shaped skeletal piece is present anteriorly, but it is asymmetrical; the left half is slender, elongated and curved; the right, short and relatively thick. A hook ("Haken") is present at the apex of the V-piece and a system of parallel supporting fibers continue posteriorly from the halves of the V. The hook is articulated with the V-piece and may be moved by a bundle of myonemes that lie parallel to the slender half of the V. The *Radiophrya* plan is departed from only as regards the asymmetry of the V-piece.

The skeletal arrangement in *lumbrici* is as follows, according to Heidenreich: The left half of the V-piece is absent, so that the attachment organelle consists only of a hook which is articulated with the slightly bent right half of the V-piece ("Grundstück" of Stein, 1854, p. 184). But the ectoplasmic supporting fibers of the left half originate along the left antero-lateral margin of the cell quite as if the missing half of the V-piece were present! Those of the right side originate along the shaft with which the hook articulates. A group of stout myonemes for moving the hook occupies the position of the missing half of the V-piece; these are the structures that were evidently mistaken by Stein (1854) for a fold along the left antero-lateral margin.

In *M. asymmetrica* the *Radiophrya* plan has undergone further changes. The hook, as said, is immovably fused with the shaft, which appears to be the equivalent of the right half of the V-piece, the left half of which is absent. Myonemes for moving the hook are absent. The supporting fibers of the left side converge anteriorly and bend to the right, so that all of the fibers arise from the right side along the right half of the V-piece. A small area on the right side is devoid of fibers and a group of fibers arises at the posterior end of the shaft. The fibers generally are distinctly shorter than those of *falcifera* and *lumbrici*, to judge by Heidenreich's figures.

These characteristic features of the skeletal elements, together with the vesicular structure of the micronucleus, seem adequate to warrant the description of my specimens from *Eisenia* as a new species.

Ciliation: M. asymmetrica, like other Astomata, is powerfully ciliated. The cilia are arranged in from 100 to 120 longitudinal rows which are spaced at intervals of 1μ around the body. As regards their origin anteriorly, the rows, like the supporting fibers, show an asymmetrical arrangement, in that all of them, whether on the dorsal or ventral surface, begin along the right anterior margin of the cell body near the shaft of the hook (figs. 1 and 2). Hence, all the rows of the left half of the body surface diverge from the mid-line near the base of the hook, as do the fibers of the left side. The origin of the dorsal and lateral rows of the right side is shown clearly in figure 2. Posteriorly, the dorsal and ventral rows show little or no convergence toward the mid-line, but end independently along the truncated posterior border (fig. 1). In general, the cilia measure 7μ in length, but those at the posterior end attain a length of 10μ, while those of the antero-ventral depression are only 4 to 5μ long. The ciliate, upon removal from its host, sometimes swims freely and spirals counterclockwise, but more commonly it creeps continuously along the substratum.

Vacuoles: In the cytoplasm of each lateral half of *M. asymmetrica*, there is a longitudinal row of from 3–6 vacuoles (figs. 1 and 7–11). Four seems to be the usual number. They lie dorsally in the endoplasm, but very near the ectoplasm (fig. 2). They are not always spaced at regular intervals in the row and sometimes their arrangement into rows is seriously disturbed. Some variations in their arrangement are shown in figures 7–11. In structure and position they resemble contractile vacuoles. In a few specimens, examined in earthworm coelomic fluid, I have observed incomplete and independent contractions of some of the vacuoles, but in intestinal contents diluted with distilled

water, Knop solution, Locke's solution and other fluids I have never observed their contraction. No doubt their failure to contract is the result of the unfavorable conditions of observation, and I have no doubt that under normal and favorable conditions of life they are contractile. Similar vacuoles occur in *lumbrici* and *falcifera;* Cépède (p. 402) describes their contraction in *lumbrici*, mentioning in particular their lack of synchronism, but he does not describe their contraction in *falcifera.*

"Silver line system:" Treatment with silver nitrate employing the methods of Klein (1926) and Gelei (1935), reveals a "silver line system" (fig. 5) which recalls that of *Paramecium* (Klein, 1926a). The basal granules (BG) of each row are connected by a longitudinal fibril (LF), the function of which is probably conductile. There is also a system of polygons (P), which recall Klein's "indirectly connected" conductile system in *Paramecium*, although the polygons are less regular in outline than in *Paramecium* and the number of basal granules to each polygon varies. Lund (1933) has shown that the outlines of the polygons in *Paramecium* are merely pellicular ridges, not fibrillae, and that each polygonal area is a pellicular depression with a single cilium at its center. I am of the opinion that the polygons of *Metaradiophrya* are likewise pellicular differentiations, since relief staining with nigrosin shows areas that seem to correspond to the polygons of the silver method.

DIVISION IN METARADIOPHRYA ASYMMETRICA N. SP.

The fact that the process of division has never been completely described to my knowledge in *Metaradiophrya* seems to warrant the following somewhat detailed account.

In *M. asymmetrica* fission is transverse but unequal. The plane of division first appears between the posterior and middle thirds of the cell body (fig. 6). (A similar position of the fission plane is shown in Heidenreich's single figure of division in *lumbrici*—Pl. 7, fig. 11.) In the early stages the anterior daughter cell or primite is, therefore, twice as long as the posterior cell or satellite. In volume it is more than twice as large, in view of the thinness of the satellite as measured dorso-ventrally (fig. 12). While the fission plane is being established in the cytoplasm, the karyosome becomes spindle-shaped and stains less intensely (fig. 6), but there is never a dissolution of the micronuclear membrane during division.

Soon the karyosome becomes resolved into a myriad of chromatin

granules within the enlarged and slightly ellipsoidal nuclear membrane. The granules are shown in figures 7 and 13 at the equator of the division spindle. Undoubtedly they are valid chromosomes, some of which appear to be rod-shaped, but attempts to count them were of no avail because of their small size and great numbers. At this stage of division (metaphase), the cytoplasmic constriction deepens, but the macronucleus shows no evidence of division (fig. 7). The micronucleus measures about 8.5μ by 7μ.

Next, the chromosomes begin to migrate to opposite ends of the spindle and a slight constriction appears in the macronucleus (figs. 8 and 14). When the chromosomes arrive at the ends of the spindle, they lose their identity by assembling in a spherical mass which soon will be the compact karyosome of the resting micronucleus (figs. 9 and 15). In the meantime the micronuclear membrane pinches in two, the spindle disappears and the cytoplasmic and macronuclear constrictions deepen (fig. 9). Then the macronucleus pinches in two and the original resting condition of the micronucleus is restored (fig. 10). The developing hook (DH) of the satellite appears in the ectoplasm at the extreme anterior end of the cell, but the satellite still remains attached to the primite.

Finally, when the hook and supporting fibers attain their full development in the satellite, the thin cytoplasmic connection between the two daughter cells is severed and they separate. The condition just before their separation is shown in figure 11.

The conditions illustrated in figures 10 and 11 apparently persist for many hours, for relatively little difficulty is experienced in finding late division stages. On the other hand, the stages shown in figures 6–9 are evidently passed through rapidly, for they were found only after long-continued search through many scores of hosts. Should the satellite separate from the primite before its attachment hook is fully developed and presumably before its thigmotactic responses are established, it would surely be swept out of its host to perish. Therefore, the primite retains the original attachment hook and supporting fibers without change during division, while the satellite remains attached until it acquires a fully developed hook. It grows in the meantime and upon separation nearly equals the primite in size.

The fact that the satellite continues to grow throughout the entire division process is evident from an inspection of figures 6–11, which are drawn to the same scale, but it is even more evident when actual dimensions are considered. For example in the dividing specimen of figure

6 the primite measured 114μ in length, the satellite, 61μ; the ratio of primite length to satellite length was, therefore, 114:61, or in simpler terms, 2:1.07. An inspection of figure 12, which shows a fixed unmounted dividing individual in side view, shows that here too the primite had twice the length of the satellite. In the metaphase shown in figure 7, the ratio was 108:65 = 2:1.12; i.e., the satellite was relatively longer. In figure 8 (anaphase), it was 102:63 = 2:1.23; in figure 9 (late anaphase), it was 102:72 = 2:1.41; in figure 10, 88:74 = 2:1.68; and in figure 11, 86:78 = 2:1.88. This series of measurements made from six different individuals is misleading in one respect; it suggests a decrease in size in the primite as division proceeds. This apparent decrease is merely an accidental result of the chance selection of the series of specimens to be drawn. In reality, dividing specimens vary greatly in length, and the primite in different specimens in the late stages of division (similar to fig. 11) may vary from 80–120μ in length, the satellite from 75–110μ.

DIAGNOSIS

Genus Metaradiophrya Heidenreich, 1935

The following enumeration of the characters of the genus is based on original observations on one species and on the published descriptions of the two remaining species. It is given here in order to amplify the somewhat incomplete description furnished by Heidenreich.

Astomatous ciliates (Family Hoplitophryidae) occurring in the intestine of Lumbricidae. Body dorso-ventrally flattened; anterior end rounded; posterior end rounded or truncate; lateral margins parallel; dorsal surface slightly convex, ventral surface flattened or slightly concave; with a depression in the antero-ventral surface the suctorial function of which is questionable. Length, 115–150μ; width, 55–70μ. Macronucleus: Median, elongate, cylindrical; dimensions, 100μ by 7μ. Micronucleus: Fusiform, ovoidal or spherical; well to right of macronucleus. Skeletal elements: Anteriorly in the mid-ventral line a chitinous hook for attachment; hook articulated with or fused with a chitinous shaft in the ectoplasm of the right anterior margin or with a similar shaft bearing a slender extension along the left anterior margin; in the ectoplasm of the antero-ventral surface, a system of longitudinal supporting fibers. Contractile vacuoles: Two longitudinal rows of about four vacuoles each; located dorsally between macronucleus and lateral margins of cell; vacuoles feebly contractile or non-contractile. Ciliation: Uniform, dense, powerful; cilia in longitudinal rows spaced at intervals of 1μ around the body. Reproduction by transverse

unequal fission, the anterior daughter cell being larger than the posterior. Hosts: *Lumbricus terrestris, L. rubellus, Eisenia foetida* and *Allolobophora caliginosa* (Europe); *Eisenia lönnbergi* (U. S. A.).

Three species.

Metaradiophrya asymmetrica n. sp.

Micronucleus: Spherical, vesicular; diameter 3.5–5μ; with a compact central karyosome measuring 2–2.5μ in diameter and containing all of the chromatin; located well to right of macronucleus just within the posterior half of cell body. *Attachment hook:* Anteriorly in the mid-ventral line a posteriorly directed chitinous hook for attachment; length, 10μ; hook continued into a chitinous shaft in ectoplasm of right antero-lateral margin; dimensions of shaft, 25–30μ by 2μ; hook immovably anchored in ectoplasm by shaft; myonemes absent. *Supporting fibers:* In the ectoplasm of the depressed antero-ventral surface a group of 25–30 longitudinal fibers, all of which arise from the *right* antero-lateral margin along the shaft of the hook. Most of them proceed toward the left, then posteriorly; they decrease in length from left to right (40μ–7μ) across the depression. With an area devoid of fibers in the right half of the depression; with a group of 7–9 short fibers that continue posteriorly from the end of the chitinous shaft. *Habitat:* Middle third of the intestine of the earthworm *Eisenia lönnbergi*.

Metaradiophrya asymmetrica differs from *M. lumbrici* (Dujardin) and *M. falcifera* (Stein) with respect to the structure of the micronucleus and the arrangement of the skeletal elements (attachment hook and supporting fibers). In *lumbrici* and *falcifera* the micronucleus is fusiform or ellipsoidal and compact, and the hook is articulated with its shaft so that it may be moved by special myonemes. In *falcifera* the stout shaft of the right side is continued as a slender rod along the left antero-lateral margin. In *lumbrici* the entire antero-ventral surface is traversed by parallel longitudinal fibers; their arrangement is bilaterally symmetrical even though the shaft of the attachment hook is on the right side. In *falcifera* there is a similar symmetrical system of parallel fibers which arise along the entire length of the bilateral piece that supports the hook.

SUMMARY

The astomatous ciliate *Metaradiophrya asymmetrica* n. sp. (Hoplitophryidae) is found in the middle third of the intestine of the earthworm *Eisenia lönnbergi*. Of 400 worms examined, 60% were infected.

Its structure and method of reproduction by transverse unequal

fission are described and the points in which it differs from *M. lumbrici* and *M. falcifera* are enumerated and discussed.

Neither encystment nor conjugation was observed, and its method of transmission from host to host remains to be ascertained.

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LITERATURE CITED

AUNAP, E. 1927. Eine Methode, Infusorien auf dem Objektträger zu fixieren und zu färben. Arch. f. Protistenk. **60:** 193–196.

BEERS, C. D. 1937. A method for the sectioning of protozoa en masse. Science **86:** 381–382.

CÉPÈDE, C. 1910. Recherches sur les infusoires astomes. Arch. de Zool. Expér. et Gén. Sér. 5, **3:** 341–609.

CHEISSIN, E. 1928. Vorläufige Mitteilung über einige parasitische Infusorien des Baikal-Sees. C. R. de l'Acad. des Sciences de l'URSS. 295–299.

——— 1930. Morphologische und systematische Studien über Astomata aus dem Baikalsee. Arch. f. Protistenk. **70:** 531–618.

DIESING, K. M. 1866. Revision der Prothelminthen. Abtheilung: Amastigen. Sitzungsb. der K. Akad. der Wiss. Wien **52:** 505–579.

DUJARDIN, F. 1841. Histoire naturelle des zoophytes. Infusoires. Paris.

GELEI, J. VON 1935. Eine neue Abänderung der Klein'schen trockenen Silbermethode und das Silberliniensystem von Glaucoma scintillans. Arch. f. Protistenk. **84:** 446–455.

HEIDENREICH, E. 1935. Untersuchungen an parasitischen Ciliaten aus Anneliden. Teil I: Systematik. Arch. f. Protistenk. **84:** 315–392.

KLEIN, B. M. 1926. Über eine neue Eigentümlichkeit der Pellicula von Chilodon uncinatus Ehrbg. Zool. Anz. **67:** 160–162.

——— 1926a. Ergebnisse mit einer Silbermethode bei Ciliaten. Arch. f. Protistenk. **56:** 243–279.

LUND, E. E. 1933. A correlation of the silverline and neuromotor systems of Paramecium. Univ. Calif. Publ. Zool. **39:** 35–76.

ROSSOLIMO, L. L. 1926. Parasitische Infusorien aus dem Baikal-See. Arch. f. Protistenk. **54:** 468–509.

——— AND PERZEWA, T. A. 1929. Zur Kenntnis einiger astomen Infusorien: Studien an Skelettbildung. Arch. f. Protistenk. **67:** 237–252.

SMITH, F. 1917. North American earthworms of the family Lumbricidae in the collections of the U. S. National Museum. Proc. U. S. Natl. Mus. **52:** 157–182.

STEIN, F. 1854. Die Infusionsthiere auf ihre Entwickelungsgeschichte untersucht. Leipzig.

——— 1860. Über die Eintheilung der holotrichen Infusionsthiere und einige neue Arten und Gattungen dieser Ordnung. Sitzungsb. der K. Böhm. Gesell. der Wiss. Prag. 2. Halbj.: 56–62.

STEIN, F. 1861. Über ein im Darmkanal von Regenwürmern aufgefundenes neues Infusionsthierchen (Hoplitophrya falcifera). Ibid. 1. Halbj.: 42–43.

STEPHENSON, J. 1930. The Oligochaeta. 978 pp. Oxford University Press.

EXPLANATION OF PLATES 10 AND 11

The writer is indebted to Mrs. Cecil Johnson and Mr. D. D. Ritchie for assistance in the preparation of the figures.

ABBREVIATIONS

AF, area of right antero-ventral surface that is free of fibers; BG, basal granule; CR, longitudinal ciliary rows; CV, contractile vacuole; D, depression or excavation in antero-ventral surface; DH, developing hook of satellite; EC, ectoplasm; EN, endoplasm; F, supporting fibers of left antero-ventral surface; H, attachment hook; LF, longitudinal fibril connecting the basal granules; MA, macronucleus; MI, micronucleus; P, polygonal area on surface brought out by silver treatment; S, shaft of hook; TF, tuft of supporting fibers on right side at end of shaft.

PLATE 10

Metaradiophrya asymmetrica n. sp.

Fig. 1. Ventral view of medium-sized individual (135μ x 55μ) fixed in Schaudinn's fluid and stained in Mallory's anilin blue-orange G-acid fuchsin. Specimens undergo very little distortion upon fixation in Schaudinn's or Bouin's fluid, so that the normal shape is fairly accurately represented. The figure shows the correct number of ciliary rows and supporting fibers. Camera lucida. × 800.

Fig. 2. Free-hand drawing of medium-sized living individual to show normal shape as viewed from right side. Micronucleus supplied from stained specimens. × 800.

Fig. 3. Free-hand drawing of maximum-sized living individual viewed from right side. To show the thinness of the posterior half and the concavity of the ventral surface in large specimens. Length, 160μ. × 350.

Fig. 4. Cross section through anterior end of animal at level of supporting fibers. The absence of a peripheral ectoplasmic thickening and the presence of cilia over the entire ventral surface indicate that this region does not function as a sucker. × 800.

Fig. 5. Portion of surface of specimen treated with silver nitrate according to Klein's method to show the surface markings (polygons), basal granules and longitudinal fibrils that connect the granules. × 5000.

PLATE 11

Metaradiophrya asymmetrica n. sp.

Fig. 6. Early division stage; dextro-ventral view. Note that the plane of fission is between the middle and posterior thirds. (In figures 6–11 no attempt has been made to show all of the ciliary rows and supporting fibers.) Camera lucida. Bouin; Delafield's haematoxylin. × 425.

Fig. 7. Division; ventral view; micronucleus in metaphase. Camera lucida. Bouin; iron haematoxylin. × 425.

Fig. 8. Division; ventral view; micronucleus in anaphase; slight constriction of macronucleus. Camera lucida. Bouin; Delafield's haematoxylin. × 425.

Fig. 9. Division; ventral view; micronucleus in late telophase; division of macronucleus. Camera lucida. Bouin; Delafield's haematoxylin. × 425.

Fig. 10. Division; ventral view; hook developing in the posterior daughter cell (satellite). Camera lucida. Schaudinn; iron haematoxylin. × 425.

Fig. 11. Late division stage; dorsal view; satellite ready to separate from primite. Camera lucida. Schaudinn; Mallory's triple stain. × 425.

Fig. 12. Dividing specimen from right side (stage of fig. 8) to show small size of satellite (left) as compared with primite. Camera lucida; drawn unmounted in Bouin's fluid to eliminate possibility of compression by cover glass. × 350.

Fig. 13. Micronucleus of specimen shown in figure 7; enlarged to show spindle fibers and appearance of chromosomes at metaphase. × 1750.

Fig. 14. Micronucleus of specimen shown in figure 8. × 1750.

Fig. 15. Dividing micronucleus of specimen shown in figure 9. Chromosomes becoming resolved into condition of the resting karyosome; portion of dividing macronucleus alongside. × 1750.

PLATE 10

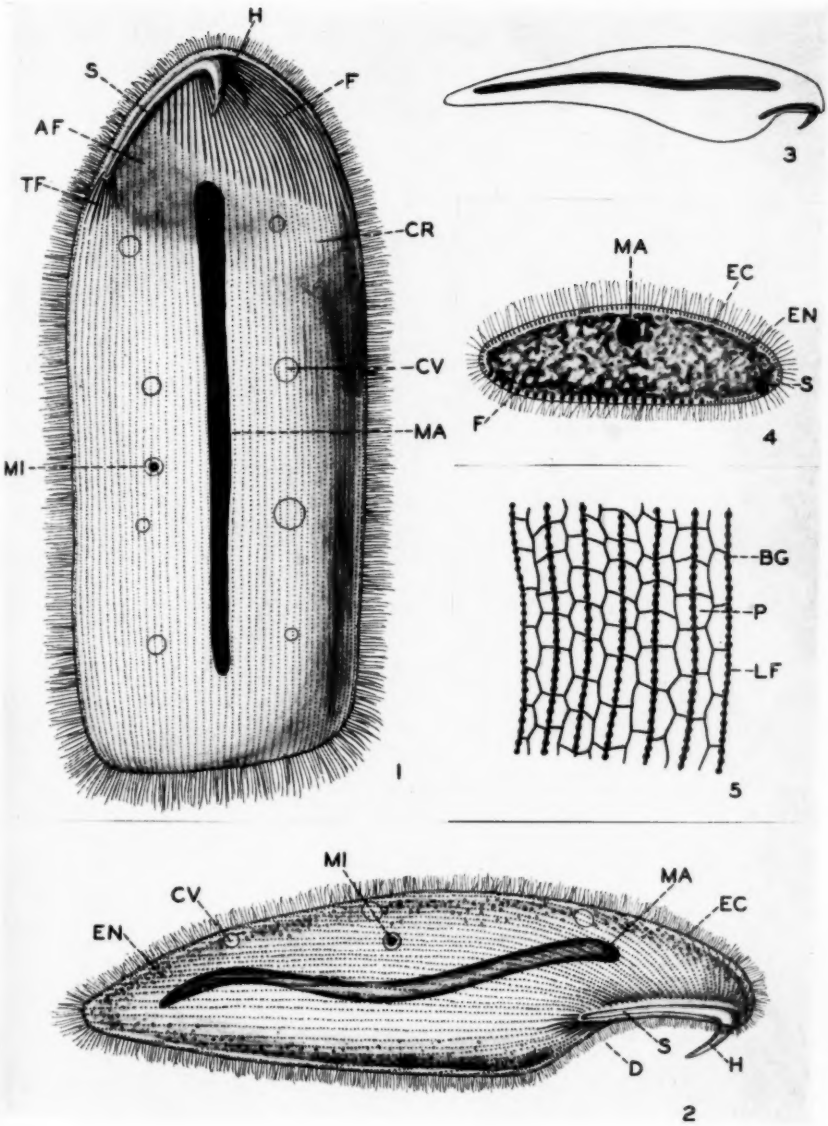
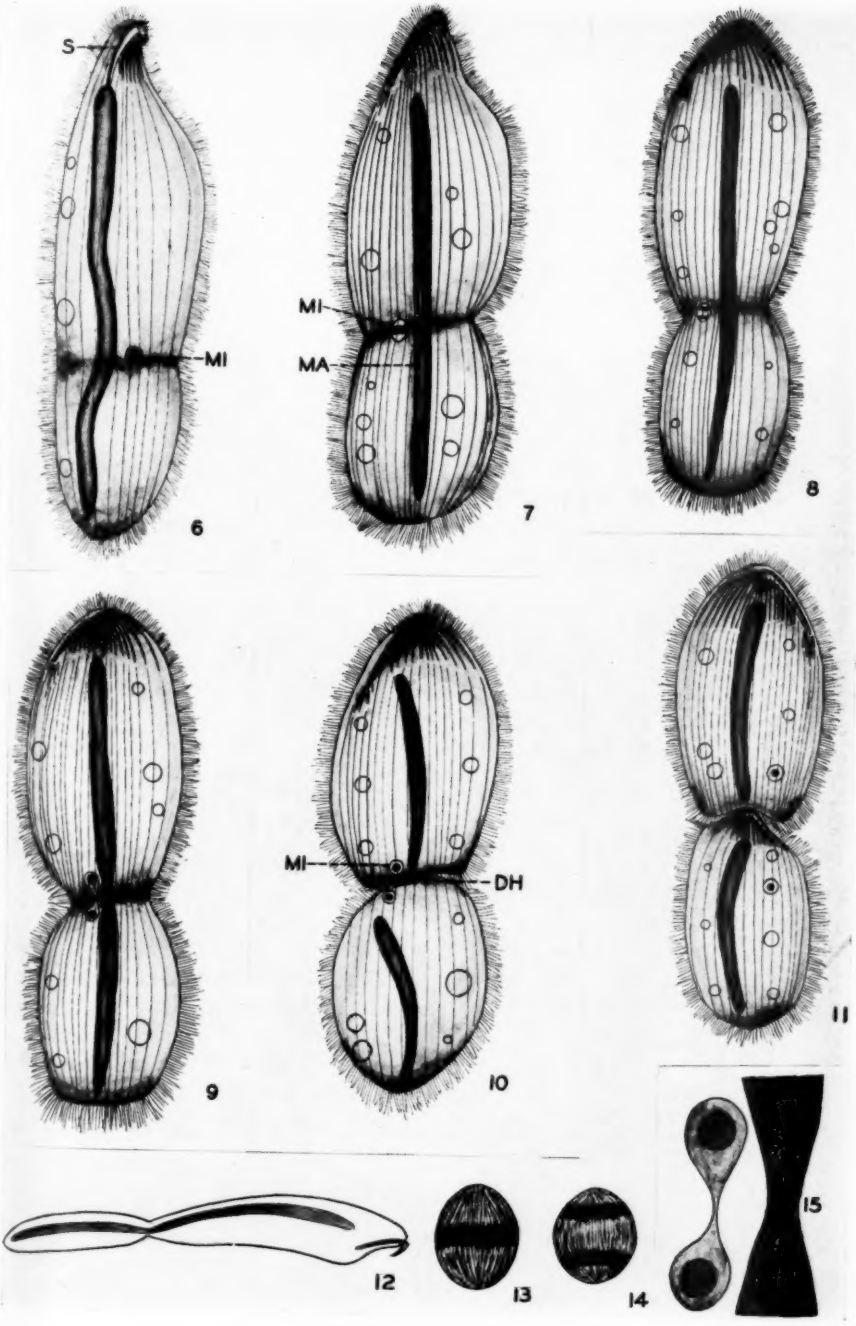


PLATE 11



MORE PRIMITIVE MOSS-MITES OF NORTH CAROLINA—III

By Arthur Paul Jacot

Plates 12 and 13

The species of Oribatidae here described are Parhypochthoniinae and Hypochthoniinae as delimited in my first paper of this series (4). I find it advisable to segregate in a separate tribe the three genera of Parhypochthoniinae in which the anteriormost transverse row of notogastral bristles comprises eight bristles, namely: the *Palaeacarini* with Palaeacarus as type.* These genera may be separated by means of the following key:

Key to Genera of Palaeacarini

Dorsum of abdomen crossed by two transverse folds.....*Aphelacarus*
Dorsum of abdomen crossed by but one complete transverse fold
Palaeacarus
Dorsum of abdomen without transverse folds.....*Acaronychus*

Figures accompanying this paper represent the animals as seen in balsam mounts, rather than depict details of morphology. Types are to be deposited at the National Museum.

Palaeacarus appalachicus sp. nov.

Figures 1, 2

Differs from *P. araneola* (2, p. 417, figs. 5-7) in having longer, stouter bristles; simple bristlelike pseudostigmatic organs; a normal number of abdominal bristles; more attenuate, mesally curved maxillae (figure 2); and finely ciliate bristles b2, b3, d3, and e1 (the eight largest of the notogaster); ungues with only two (subequal) hooks of which the lateral are a little longer. Size of extended female 0.368 mm., breadth 0.167 mm.

Thus this species is more primitive (except in the modification of the

* If Archeonothrus belongs in this tribe—a point impossible to determine from Trägårdh's very insufficient figures (7)—the name of the tribe will have to be changed to Archeonothrini.

maxillae). The anal covers bear but four bristles, the adanals five. The genital covers bear seven bristles which are not quite linearly arranged, in mesal row, and two in lateral row. The aggenital (?) bristles number three. Thus the genital area is the same as in Acaronychus. Notogastral bristles d4 are on the rim of the notogaster on the ventral face.

This is the first record of this genus from the United States. The females bear one rather globular egg at a time (possibly two).

This species differs from *P. hystricinus* (7) (the genotype and most closely related described species) of Sweden, in the much shorter cephaloprothorax; much shorter bristles c1; much longer bristles d3; in having one pair less of conspicuous dorsoabdominal bristles; and, possibly, cilia all around the eight major bristles of dorsum of abdomen.

Cotypes: Thirty adults and immatures from litter of seventy year old old-field pine-oak woods, laboratory grounds, Bent Creek Experimental Forest, Buncombe Co., N. Car.; taken September 13th, slide 34F3.2-2.

Acaronychus trägårdhi longipilus subsp. nov.

Differs from the species (2, p. 421, figs. 8–10) in that all of the long bristles are stout, weakly and distantly barbed (except rostrals); upper exopseudostigmatic bristles are strongly bent; dorsoposterior bristles c1 are very long (three times length of other bristles), weakly and distantly barbed; the clavate bristles of posterior end of abdomen (d1) are as long as tibia or genual, longer than either of the two trochanters. The location of the bristles is the same.

Cotypes: Six specimens from pine litter, of uneven-aged old-field, Stadley Hill, six miles south of Asheville, N. Car.; taken October 30th, slide 34F15.23.

One of the outstanding problems in the study of the Oribatidae is the homology of the notogastral bristles. Since the Parhypochthoniinae include the most primitive species they should indicate the primitive condition. The outstanding contribution of the species of Aphelacarus, Palaeacarus, and Acaronychus, that is the tribe Palaeacarini, is the presence of eight bristles in the anterior transverse row (row *a*). The fourth or lateralmost bristle (a4) is quite small but quite evident. Unlike other Parhypochthoniinae, row *a* is followed (posteriorly) by a transverse fold or suture. One would expect another such fold behind the second transverse row, a condition which apparently is common

to many other Oribatidae, but there is only a partial fold, best developed on the sides. It indicates that the eight bristles of row *b* have already become strongly staggered (figure 1). So much are these bristles displaced that their homology is not clear except by careful comparison of all known species. It then becomes evident that the notogastral bristles are displaced anteroposteriad much more easily than lateromesad. Accepting this as a principle we can designate the anteriormost large ciliate bristle of figure 1 as b3 and the next one posteriad as b2. Bristles b1 are always anteriormost and closest to median plane. The bristles of row *c* of figure 1 are: the minute bristle (c2) at foot of the large ciliate bristle (d3), the bristle posterolaterad of this pair (c4), while the others are obvious. A second *principle* now becomes apparent, namely, alternate bristles of a transverse row tend to migrate together. The minute bristle at foot of the posteriormost large ciliate bristle (e1) is d1. Bristles d4 are on ventral aspect.

Brachychthonius latus (5, p. 248)

In the original description reference to the cotypes was overlooked. The sixty-eight cotypes are from the same sample as the specimens mentioned but are on slide 34F9.2–6.

Brachychthonius prior sp. nov.

Figure 3

Notogastral bristles short, fine, the position of those of anterior transverse plate of dorsum of abdomen as in *B. perpusillus* (5, p. 1, pl. 20, fig. 1) (figure 3); thus resembling *B. bifurcatus* but pseudostigmatic organ head pointed, and the barbs quite distinct, that is, of the usual type; body smooth and puffy, the cephaloprothorax with a small crescent beneath exopseudostigmatic bristles; color pale yellow; size medium (for the genus): length of ovigerous females 0.19 to 0.22 mm. (depending on extension of midthoracic region), breadth 0.096 mm. Thus relatively longer than *B. perpusillus*.

Cotypes: Ninety-one specimens from leaf litter, Robinia stand, Copper Basin, Polk Co., Tenn.; taken November 1st, 1935, by H. J. Loughead, slide 35FC1–5.

Brachychthonius attenuatus sp. nov.

Figure 9

Bristles short, simple (as *B. bifurcatus*) (5), typically located; no sculpturing; pseudostigmatic organ head dense, nearly smooth, very

slender (attenuate); nearly colorless; size rather small: length 0.15 to 0.16 mm., breadth 0.09 to 0.1 mm.

Cotypes: Six specimens from oak litter, west slope of ridge above Poplar Cove, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken July 29th, slide 35F7.2–2.

BRACHYCHOCHTHONIUS gen. nov.

Resembling Brachychthonius but with dorsum of abdomen divided into three *longitudinal* areas by two longitudinal ridges which, in dorsal aspect make the posterior end of abdomen appear bituberculate; cephaloprothorax and dorsum of abdomen usually sculptured; contour of cephaloprothorax otherwise indented so as to give it the appearance (in dorsal aspect) of possessing sclerotized ridges which are in reality the surface of the indentations seen on edge; bristles usually short or highly modified; both shoulder bristles on a distinct oval plate (figure 4); notogastral bristles b2 usually on lateral edge of abdomen; posterior segment of abdomen with only six pairs of bristles on dorsal face (the seventh pair is on posterior end below the mesal pair).

Type: *Brachychochthonius jugatus* sp. nov.

Brachychochthonius jugatus sp. nov.

Figures 10, 11

Middle area of cephaloprothorax and dorsum of abdomen sculptured by a series of irregular, often angular, narrow, unequal, elongate ovals, each with a median ridge (figure 10); anterior end of cephaloprothorax indented by coarse scallopings; bristles of notogaster short, those of posterior end quite clavate (figure 10); in lateral aspect edge of rostrum is simply carinate (figure 11), the lamellar bristle area angular but not prominent, the profile rather flat; color practically lacking; size rather small: total length 0.16 mm., breadth 0.08 mm.

Brachychochthonius laevis sp. nov.

Figure 5

Body without sculpturing; longitudinal ridges of dorsum of abdomen with their posterior tubercles present; the indentations of anterior end of cephaloprothorax also present (figure 5); all bristles (except rostral) short, those of posterior end of abdomen clavate. Thus resembling an unsculptured *B. jugatus*. The females bear the usual solitary egg. Color yellowish; size somewhat small: total length of ovigerous females 0.169 mm., greatest breadth 0.083 mm.

Cotypes: Thirteen specimens from leaf litter of Robinia stand, Copper Basin, Polk Co., Tenn.; taken November 1st, 1935, by H. J. Loughead, slide 35FC1–6.

Brachychochthonius berlesei erosus subsp. nov.

Figures 12–14

Sculpturing of cephaloprothorax similar to that of *B. jugatus* but the anterior end less indented; a single large median indentation gives that area the dorsal aspect of having a single transverse ridge (figure 12); central area of notogaster sculptured with oval depressions resembling corrosion or solution pits (hence the name); notogastral bristles short, those of posterior end barely if at all clavate (figure 14). The sculpturing varies with the individual or the age, for in these genera there is a very gradual transition between the different nymphal and the adult stages. The general tendency is for reduction of sculpturing, especially on cephaloprothorax (compare figures 12 and 14). In lateral aspect, edge of rostrum is bicarinate (figure 13), the lamellar bristle area is more bulby, and the profile more irregular (figure 13); color pale (nearly colorless); size somewhat small, total length 0.174 mm., greatest breadth 0.086 mm.

Cotypes: Thirty-three specimens from Liriodendron litter of a northeast cove, east end of Shut-in-Ridge, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken October 1st, 1934, slides 34F8–9.

Although this form and *B. jugatus* are found in the same handful of litter, *B. b. erosus* is confined to the upper drier layer (the L-layer), while *B. jugatus* is found in the layer below it (the F-layer) characterized by greater moisture, much more fungus, and leaves more or less fragmented.

Brachychochthonius berlesei comb. nov. (8, p. 160, fig. 11; 1, p. 220, pl. 19, fig. 39) differs somewhat in sculpturing and in the shape of the notogastral bristles.

Brachychochthonius rostratus comb. nov.

Figure 15

In lateral aspect the rostrum appears very large, almost as high as the cephaloprothorax and the sides of the latter are more sculptured than in the preceding species (figure 15). The rostral bristles are not distinguishable.

Brachychochthonius italicus spiciger comb. nov.

Although the longitudinal ridges of the dorsum of the abdomen are not as marked in this species as in the preceding, so that the posterior end of the abdomen (as seen in dorsal aspect) is usually smoothly rounded, it belongs in this genus. Emaciated or much dried out specimens show the ridges and posterior tubercles; the short bristles, dorsal sculpturing, and sculpturing of the top of the cephaloprothorax indicate this relationship. The figure of this form in the preceding paper (5, pl. 20, fig. 7) should have notogastral bristles b2 removed to lateral edge of abdomen close to the diagonal line formed by the encroachment of the middle segment.

Brachychochthonius zelawaiensis comb. nov.

Figure 6

Specimens received from Max Sellnick are identical with individuals from the mountains of North Carolina. As Sellnick's figure (6, p. 348, fig. 11) might lead one to regard the top of the cephaloprothorax as similar to that of Eobrachychthonius, I include a figure showing the ridges and their enclosures. Besides the six pairs of bristles on the posterior segment of the dorsum of the abdomen, there is a pair at the posterior end, barely visible under the mesal pair, and the usual ventral pair near edge of adanal covers.

This species is easily recognized by the large, clavate-spatulate bristles. In the figure some of the bristles are omitted in order to make the sculpturing more distinct. In my specimens, mounted in balsam, the bristles on the dorsal face of the animal are not discernible. In Sellnick's specimens, mounted in Berlese-Faure medium (a gum arabic base), they are quite distinct, and every line of the sculpturing is so clear and distinct that I am constrained to try again this mounting medium for small colorless or nearly colorless species. Its chief drawback,—excessive reduction in drying, is conspicuous in Sellnick's slide, which is half dried out although ringed with asphaltum. To get clarity of detail however, justifies the use of such a temporary medium—at least for part of ones material.

Brachychochthonius lydiae sp. nov.

Figures 7, 8

Closely resembles *B. zelawaiensis* in form, size, and sculpturing but differs from all described species in the shape of its bristles which are

(as seen in balsam mounts) arborescent. Figure 7 illustrates the appearance of the shoulder bristles a4, while figure 8 shows the pattern of the bristles of the posterior end of the abdomen (dorsal aspect); adanal bristles conspicuous; colorless; size small: total length of body 0.14 to 0.15 mm., breadth 0.06 to 0.07 mm.

Holotype: from litter of laurel slick, north slope of Shut-in-Ridge, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken May 8th, slide 35F1.3–4. Paratype: from pitch-pine litter of old-field, Stradley Hill, three miles north of Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken October 30th, slide 35F15.2B4.

Named after my wife who has spent many tedious hours sorting and mounting material, in addition to aiding me in a multitude of other ways, directly and indirectly.

Brachychochthonius crenulatus sp. nov.

Figure 16

Bristles rather long, simple; b3 in the primitive position; cephalothorax with precipitous sides and front,—as indicated by the dark stripe seen in dorsal aspect; sculpturing indistinct in balsam mounts, comprising chiefly scalloped patterns as in figure 16; posterior edge of abdomen crenulate; nearly colorless; size medium: length of body 0.17 mm., breadth 0.1 mm.

Of thousands of specimens of Brachychthonius and Brachychochthonius, I have but three specimens of this species. Holotype: from dogwood litter of thirty year old old-field, laboratory grounds, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken September 20th, slide 34F4.3–7.

EOHYPOCHTHONIUS gen. nov.

Hypochthoniinae with one prominent transverse fold across back of abdomen behind second transverse row of (6) bristles; ventral plate undivided, anterior end extending to midthoracic constriction, separated from dorsal plates by a distinct suture or fold of flexible skin except along posterior half where it becomes evanescent half way between bristles c4 (which are the only bristles on its edge) and d4; genital plate transversely divided.

Type: *Hypochthonius gracilis* 5, p. 251, pl. 20, fig. 9.

This genus differs from Hypochthonius in that the genital covers are transversely divided, and abut parasterna IV; the aggenital plate (as seen in ventral aspect) ends in a point at sides of genital aperture;

notogastral bristles a2 are well developed. In general it is more closely related to Eniochthonius than to Hypochthonius. In size of aggenital plates it is more primitive than Eniochthonius, for these plates get larger from Brachychthonius through Eniochthonius to Hypochthonius!

MIGRATIONS OF NOTOGASTRAL BRISTLES

Brachychthonius is supposed to be very primitive because of its "segmentation." Accepting it as such and to make it consistent with the Palaeacarini, we will recognize the eight anteriormost bristles as a1 to a4,—a3 having slipped posteriad more than the others (4, pl. 1, figs. 3, 4; 5, pl. 20, figs. 1, 7). The two posterior bristles of the anterior "segment" are b1 and b3 (as in the Palaeacarini) and the two bristles of the middle "segment" must be b2 and b4 (as in the Palaeacarini). In short this middle segment is, in part at least, a false segment which does not necessarily indicate a primitive condition. If it is a true segmental fold, then Brachychthonius is more primitive than the Palaeacarini! This notation is corroborated in the figure of the larva of Sphaerochthonius (3, p. 24, fig. 2A, 2B) where the four bristles a1 to a4 (called c1 to c3 and d3 by Grandjean) are on the anterior segment; while b1 to b2 (bristles d1, d2, e1, e2 of the figure) are on the next two segments. It is also corroborated by the change in position of bristle a3 in Eniochthonius from larva to adult (3, p. 25, fig. 3C to 3A), that is progressively more in line with bristles b1 and b3. Bristles a4 always remaining anchored in their corner.

The posterior segment possesses fourteen bristles on the dorsal face arranged as in *B. perpusillus* (5, pl. 20, fig. 1), and two on the ventral face. The eight anteriormost of these are probably the *c* group, while the other eight are the *d* group with either e1 lost or one of the *d* group lost, who can say which?

In Brachychthonius b1 and b3 are fairly close together. In Eobrachychthonius and Brachychochthonius b3 has migrated to the lateral end of the plate (compare figures 3 and 9 with figures 6, 10, 12, and 14), as had so many of the other bristles. In this respect Brachychthonius is more primitive. As to the posterior plate: in Brachychthonius c4 is peripheral while d3 is not, while in Brachychochthonius c4 is not peripheral while d3 is peripheral (using the term peripheral to designate the sides of the abdomen as viewed in dorsal aspect, which in these two genera is the lateral edge of the dorsal plates). Finally in Brachychthonius d2 is laterad of d1, while in Brachychochthonius d2 is ventrad of d1.

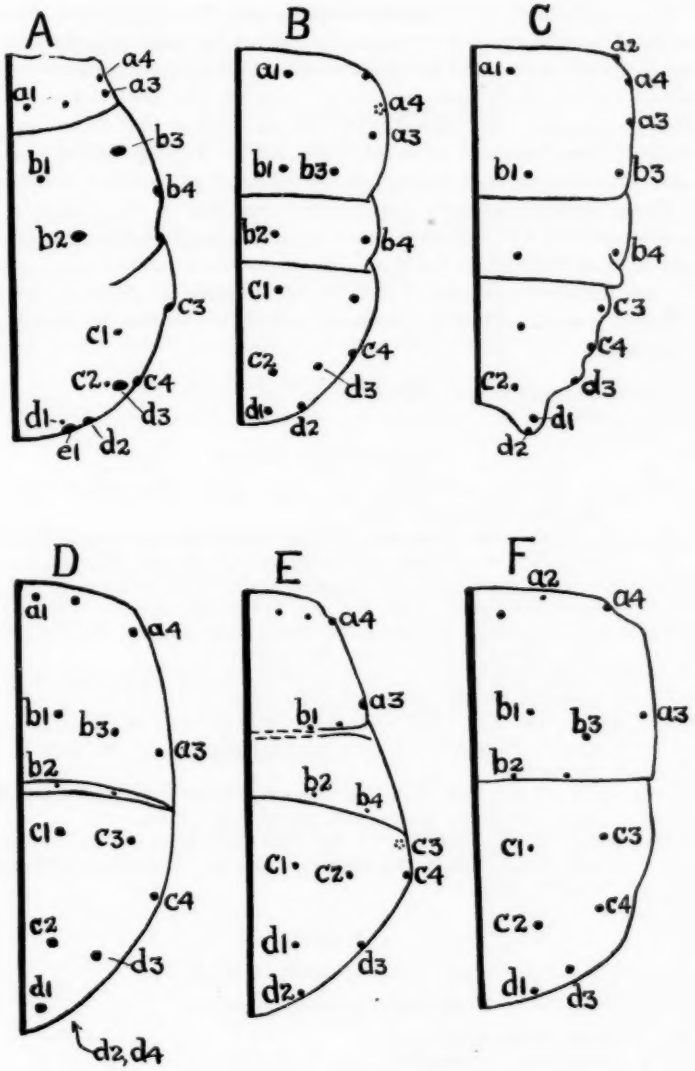


DIAGRAM OF LOCATION OF BRISTLES OF DORSUM OF ABDOMEN

A = Palaeacarus, B = Brachychthonius, C = Brachychochthonius, D = Eohypochthonius, E = Eniochthonius, F = Hypochthonius.

In Eniochthonius, Eohypochthonius, and Hypochthonius, bristles a1 to a4 and b1 to b4 have taken up similar positions, except that a3 has dropped back to be in line with b1 and b3, which must have occurred before b3 became peripheral. As for the posterior segment: Eohypochthonius resembles Brachychthonius except that d2 has become ventral; Eniochthonius is a law unto itself; Hypochthonius appears more primitive in that neither c4 nor d3 have yet become peripheral.

These modifications are graphically presented in the diagram. It is evident from all this that some bristles are more stable than others, and that of the mobile bristles, some move more rapidly than others. To put it more succinctly, a bristle may migrate at different rates in different genera. This law produces radiate in contrast to monolinear evolution.

NORTHEASTERN FOREST EXP. STATION,
NEW HAVEN, CONN.

LITERATURE CITED

1. BERLESE, ANTONIO. 1910 (Feb. 9). Acari nuovi, Manipulus V and VI. Redia **6**: 199-234, pls. 18-21.
2. GRANDJEAN, F. 1932 (June 18). Au Sujet des Palaeacariformes Trägårdh. Bull. Mus. nat. d'Hist. nat. Paris, ser. 2, **4**: 411-426, 10 comp. figs.
3. ——— 1934 (March 31). Les Organes respiratoires secondaires des Oribates (Acariens). Ann. Soc. ent. France **103**: 109-146, 17 comp. figs.
4. JACOT, A. P. 1936 (July). Some Primitive Moss-Mites of North Carolina. Jour. Elisha Mitch. Sci. Soc. **52**: 20-26, pl. 1.
5. ——— 1936 (Dec.). More Primitive Moss-Mites of North Carolina. Jour. Elisha Mitch. Sci. Soc. **52**: 247-253, pl. 20.
6. SELLNICK, MAX. 1930. Die Oribatiden (Hornmilben) des Zehlaubruches. Schrif. Phys.-ökon. Gesell. zu Königsberg i. Pr. **66,** heft 2: 324-351, 15 figs.
7. TRÄGÅRDH, IVAR. 1932 (Feb. 26). Palaeacariformes, a new suborder of acari. Arkiv för Zoologi **24B,** part 2, 6 pp., 6 figs.
8. WILLMANN, CARL. 1928 (Oct.). Die Oribatidenfauna nordwestdeutscher und iniger süddeutscher Moore. Abd. Nat. Ver. Bremen **27,** heft 1: 143-176, 15 figs.

PLATE 12

Fig. 1 × 300; all others × 630.

Palaeacarus appalachicus *sp. nov.*

Fig. 1. Dorsal aspect of abdomen.
Fig. 2. Dorsal aspect of maxillae.

Brachychthonius prior *sp. nov.*

Fig. 3. Dorsal aspect of cephaloprothorax and anterior abdominal segment.

Brachychochthonius *sp.*

Fig. 4. Lateral aspect of anterior and middle abdominal segments, showing bristles a2, a3, b3, b4 (a3 masked by rim of sclerite).

Brachychochthonius laevis *sp. nov.*

Fig. 5. Dorsal aspect of cephaloprothorax.

Brachychochthonius zelawaiensis *comb. nov.*

Fig. 6. Dorsal aspect of cephaloprothorax and anterior abdominal segment, several of the bristles omitted.

Brachychochthonius lydiae *sp. nov.*

Fig. 7. Dorsal aspect of bristle a2 (shoulder bristle).
Fig. 8. Dorsal aspect of bristles of posterior end of abdomen.

Brachychthonius attenuatus *sp. nov.*

Fig. 9. Dorsal aspect, legs and mouth parts omitted.

PLATE 13

All figures × 630.

Brachychochthonius jugatus *sp. nov.*

Fig. 10. Dorsal aspect, legs and mouthparts omitted.
Fig. 11. Lateral aspect of dorsal profile of cephaloprothorax.

Brachychochthonius berlesei erosus *subsp. nov.*

Fig. 12. Dorsal aspect of cephaloprothorax and anterior abdominal segment.
Fig. 13. Lateral aspect of dorsal profile of cephaloprothorax (slightly from above).
Fig. 14. Dorsal aspect of another individual (nymphal ?).

Brachychochthonius rostratus *comb. nov.*

Fig 15. Lateral aspect of cephalon.

Brachychochthonius crenulatus *sp. nov.*

Fig. 16. Dorsal aspect, legs and mouthparts omitted.

PLATE 12

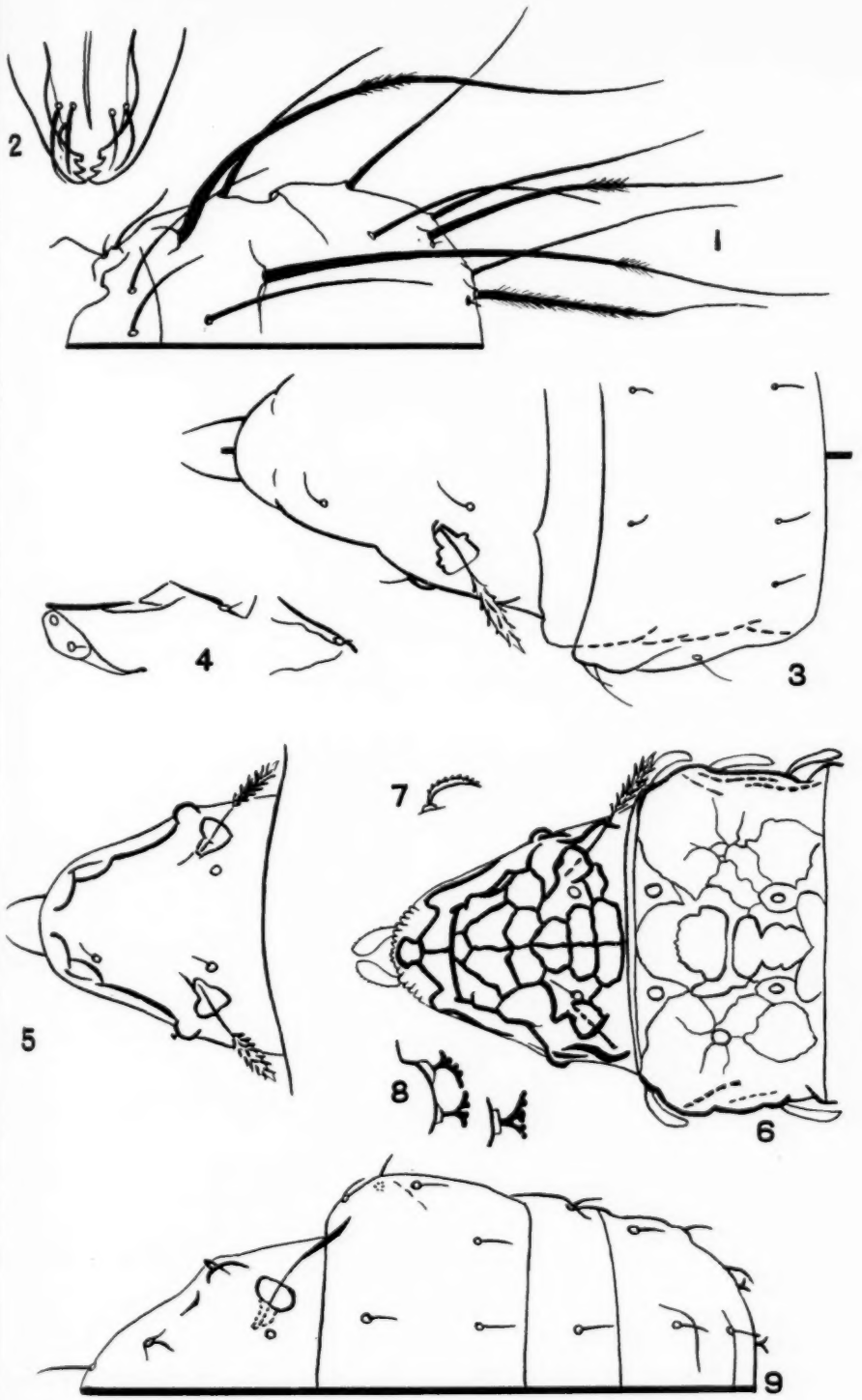
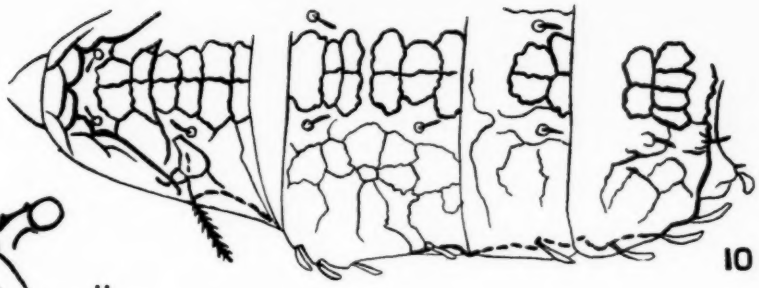


PLATE 13



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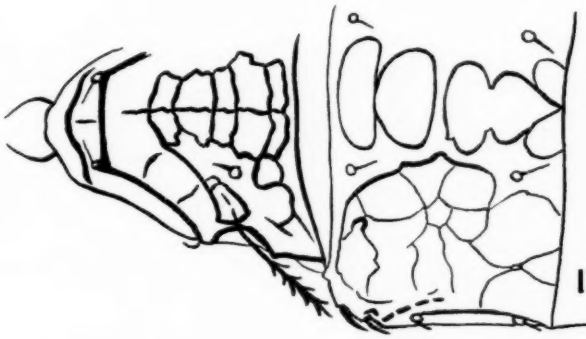

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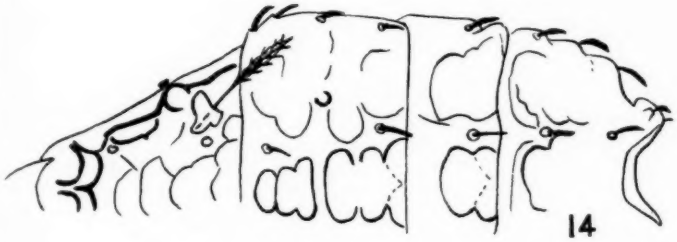

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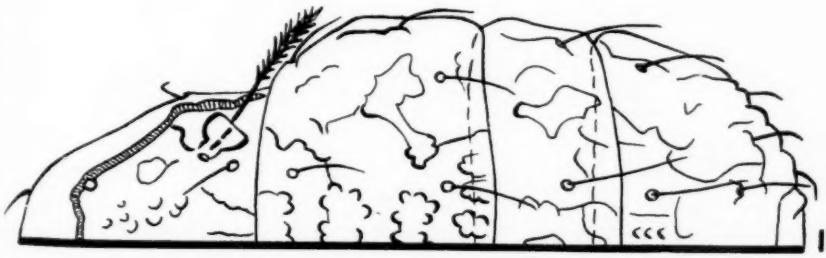


16

AGARICUS AT GAINESVILLE, FLORIDA

By William A. Murrill

Plate 14

Members of the genus *Agaricus* are always interesting because of their use as food. I find the species at Gainesville, Fla., very similar to those recorded by Prof. W. C. Coker for Chapel Hill, N. C., but with exceptions as noted in the following list:

Agaricus campester L.

Common at times, especially in spring and fall, but not nearly so abundant as in the meadows and pastures and old fields of Virginia and other more temperate regions.

Agaricus comtulus Fr.

Common in the woods here, at times appearing in patches containing hundreds of sporophores. The stipe is always rather long and slender.

Agaricus floridanus Pk.

Described from specimens collected by Dr. G. C. Fisher at De Funiak Springs, Florida, in 1910 and collected by me rarely in sandy soil both at Green Cove Springs and at Gainesville. I photographed some of the sporophores, then dried them, and ate the rest.

Agaricus pratensis Scop.

A fine edible species, but unfortunately rare here. Most of my friends prefer it under another name.

Agaricus sylvicola (Vitt.) Sacc.

A beautiful white species occurring commonly in our woods. Peck's name, *A. abruptibulbus*, is more descriptive, unless Vittadini had in mind some fair sylvan nymph.

Agaricus placomyces Pk.

Common in woods here, just as I remember it in New York and Virginia. As Coker remarks, the specimens fit the pictures.

Agaricus auricolor Krieger

Known to the older mycophagists as Curtis' almond mushroom, but he failed to describe it. I have seen it and enjoyed it here for several years. Last summer it appeared abundantly on a shaded lawn where manure mixed with sawdust had been scattered. The young sporophores are often exactly cylindric. Dried specimens are yellow like those of the horse mushroom, thus meriting the name assigned by Krieger. A full and illustrated account of this interesting species was given by Dr. W. C. Coker in his article on *Psalliota* in this Journal, vol. **43**: 249, 1928.

Agaricus diminutivus Pk.

A small form of this species with slender stipe grows sparingly in mixed oak and pine woods here, appearing in patches of a dozen or more sporophores. In shape it resembles *A. comtulus* Fr., but the cap is a pretty reddish-pink when fresh, becoming reddish-brown when dried. There is also a slight umbo at times and the fibrillose scales are always present as described by Peck.

Agaricus alachuanus sp. nov.

Pileus convex to slightly depressed, gregarious, about 3–4 cm. broad; surface dry, isabelline, with purple scales arranged in an imbricate pattern as in *A. placomyces*, not becoming darker on drying, purplish-brown on the disk; context white; lamellae as usual for the genus, almost black with age; spores subellipsoid, smooth, dark-brown, 6 x 3.5μ; stipe white, smooth, rather thick, bulbous, not exceeding 4 cm. in length; annulus ample, persistent, white, becoming yellow on drying.

Type collected by W. A. Murrill in a low spot under a laurel oak in Gainesville, Fla., August 17, 1937 (No. 15917). From our other small species, *A. comtulus* and *A. diminutivus*, this one differs decidedly in its shorter, thicker stipe and conspicuous purple scales. From small forms of *A. micromegethus*, the ample, persistent annulus would at once distinguish it. Some of my readers might like to know that Gainesville is situated in Alachua County, an Indian word more difficult to pronounce properly than to spell correctly.

Agaricus praemagniceps sp. nov.

Pileus cylindric-truncate to convex, expanding and finally depressed, gregarious, reaching fully 15 cm. in diameter; surface uniformly rosy-avellaneous when young, becoming pallid at maturity with the disk

sprinkled over with minute avellaneous fibrils; context white, scarcely changing, of good flavor but too tough and stringy for enjoyment; lamellae white when young, almost black with age; spores ovoid, smooth, dark-brown, 6 x 3.5–4μ; stipe very white, smooth, glabrous, nearly equal, abruptly bulbous, about 6–10 x 1–1.5 cm.; annulus white, single, ample, persistent.

Type collected by W. A. Murrill under a laurel oak in Gainesville, Fla., August 15, 1937 (No. 16051). Also collected by the author several other times under evergreen oaks about Gainesville in late summer or early fall. In view of its size and attractive appearance, it was quite disappointing to find it rather an exception for the genus from the standpoint of the mycophagist.

NEW COMBINATIONS

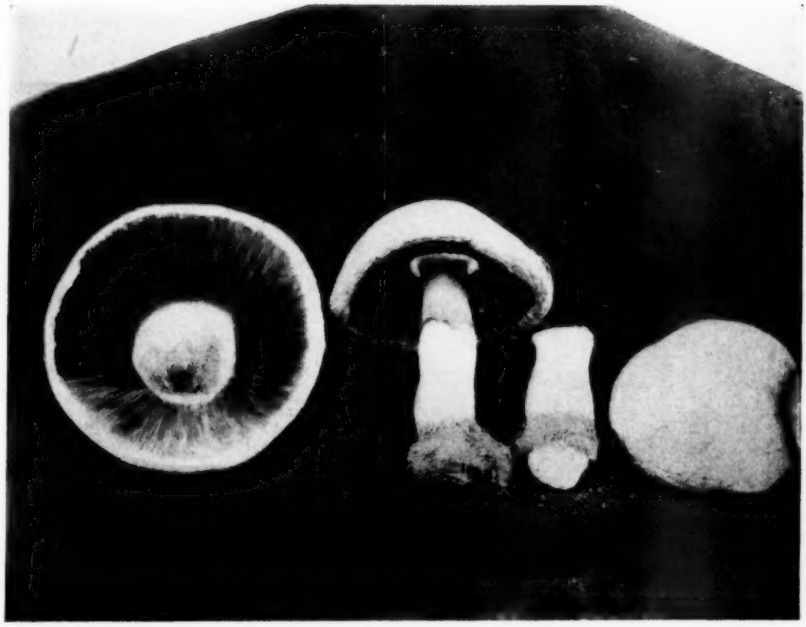
For those using a different nomenclature the following transfers are made:

Agaricus alachuanus = **Psalliota alachuana.**

Agaricus praemagniceps = **Psalliota praemagniceps.**

GAINESVILLE, FLA.

PLATE 14



AGARICUS FLORIDANUS PK. x ½
(Photograph by the author)

UNIV. OF MICH.

ATMOSPHERIC POLLEN SURVEY OF CHARLOTTESVILLE, VIRGINIA, FOR 1936[1]

By Elton C. Cocke

It is a well established fact that all true hayfever is caused by pollen. This pollen may be inhaled from the normal pollen content of the air as the victim goes about his daily duties, or it may be gotten by direct contact with flowers; the latter cases occur chiefly among gardeners and punctilious housewives who carefully arrange daisies and daffodils, goldenrods and chrysanthemums in vases about the house. By far the greater majority of cases of hayfever are caused by wind-blown pollen which invades the atmosphere from early spring to late fall. It is obvious that an accurately determined pollen survey furnishes the best clue to the hayfever potentialities of any given locality. The pollen cycle is repeated year after year with only slight variations due to seasonal conditions. Every community should, therefore, have a reliable pollen survey made and the data obtained recorded in readily available form. It is the purpose of this paper to record and discuss the pollen content of the air at Charlottesville, Virginia, during 1936, as determined by results obtained from the examination of slides exposed daily during the entire year.

Charlottesville is located in Albemarle County near the geographical center of Virginia in the foothills of the Blue Ridge Mountains. The elevation is about 500 feet above sea level. The city is more or less surrounded by low mountains which are covered by a mixed hardwood type of forest, with oak predominating. Approximately 41% of the land of Albemarle County is either in cultivation or in open pasture. Patches of scrub pine are to be found in many abandoned fields nearby.

Neff (1) listed the trees given in Table I as native to Albemarle. Their relative abundance is also given. In addition to the native species there are many exotic trees planted on the University of Virginia grounds. Paper mulberry which is common as an escape, cypress, and spruce are the only introduced genera which shed enough pollen into the atmosphere to be important in a pollen survey.

[1] Contribution from Miller School of Biology, University of Virginia.

TABLE I

Native Trees of Albemarle

COMMON NAME	BOTANICAL NAME	RELATIVE ABUNDANCE
Alder	*Alnus serrulata*	Abundant along streams
Ash, white	*Fraxinus americana*	Common
Ash, red	*F. pennsylvanica*	Common along streams
Aspen, large tooth	*Populus grandidentata*	Rare
Basswood	*Tilia americana*	Common
Beech	*Fagus grandifolia*	Common
Birch, black	*Betula lenta*	Common along streams
Birch, yellow	*B. lutea*	Common along streams
Boxelder	*Acer Negundo*	Scarce
Buckeye	*Aesculus glabra*	Rare
Cedar, red	*Juniperus virginiana*	Abundant
Cherry, wild	*Prunus serotina*	
Chestnut	*Castanea dentata*	Mostly killed out
Chinquepin	*C. pumila*	Common
Cottonwood	*Populus alba*	Rare
Cucumber tree	*Magnolia acuminata*	Rare
Dogwood	*Cornus florida*	Abundant
Elm, American	*Ulmus americana*	Common
Gum, black	*Nyssa sylvatica*	Common
Hackberry	*Celtis occidentalis*	Scarce
Hickory, mockernut	*Carya alba*	Abundant
Hickory, shellbark	*C. ovata*	Rare
Hickory, pignut	*C. glabra*	Common
Hickory, bitternut	*C. cordiformis*	Rare
Hornbeam	*Ostrya virginiana*	Common along streams
Holly	*Ilex opaca*	Common
Ironwood	*Carpinus caroliniana*	Common along streams
Locust, black	*Robinia pseudo-acacia*	Abundant
Locust, honey	*Gleditsia triacanthus*	Common
Maple, black	*Acer nigra*	Rare
Maple, silver	*A. saccharinum*	Common
Maple, red	*A. rubrum*	Abundant
Mulberry, red	*Morus rubra*	Common
Oak, white	*Quercus alba*	Abundant
Oak, red	*Q. rubra*	Abundant
Oak, post	*Q. stellata*	Abundant
Oak, chestnut	*Q. prinus*	Common
Oak, black	*Q. velutina*	Abundant
Oak, scarlet	*Q. coccinea*	Abundant
Oak, Black Jack	*Q. marilandica*	Common
Oak, Spanish	*Q. falcata*	Abundant
Oak, pin	*Q. palustris*	Common
Osage orange	*Maclura pomifera*	Common
Pawpaw	*Asimina acuminata*	Rare

TABLE I—*Concluded*

COMMON NAME	BOTANICAL NAME	RELATIVE ABUNDANCE
Paulownia	*Paulownia tomentosa*	Rare
Persimmon	*Diospyros virginiana*	Scarce
Plum, wild	*Prunus nigra*	Scarce
Pine, white	*Pinus strobus*	Abundant
Pine, Jersey	*P. virginiana*	Abundant
Pine, pitch	*P. rigida*	Common
Pine, yellow	*P. echinata*	Abundant
Redbud	*Cercis canadensis*	Abundant
Sassafras	*Sassafras variifolium*	Abundant
Service berry	*Amelanchier canadensis*	Common
Sycamore	*Platanus occidentalis*	Common
Walnut, black	*Juglans nigra*	Common
Walnut, white	*J. cinerea*	Common
Willow, black	*Salix nigra*	Common along streams

The common grasses and wind pollinated weeds of this vicinity are listed in Table II. Several species of golden rod are abundant, but since these are not generally wind pollinated they do not contribute appreciably to the atmospheric pollen.

METHODS

Microscopic slides coated with Brandt's glycerine jelly to which methylene green had been added were exposed to the atmosphere for 24 hours. At the end of the exposure period the slides were taken into the laboratory, warmed gently to drive off excess moisture, then a drop of warm glycerine jelly added and a #1 cover glass put on. The slides were exposed approximately 20 feet from the ground and were protected from sun and rain by a shelter open on two sides.

The slides were examined, all grains carefully identified, and number of each type of pollen recorded for each day. From the number of grains caught per square centimeter the pollen concentration per cubic yard was determined from formula and table given by Cocke (3) based on his revision of Scheppegrell's (4) formula. Due allowance was made for difference in size as well as wings, spines, etc., in determining the number of pollen per cubic yard.

RESULTS

Chart I and Table III give the results of the pollen concentration in number of grains per cubic yard from March 1st through October. Even though pollen was caught almost every clear day during the year,

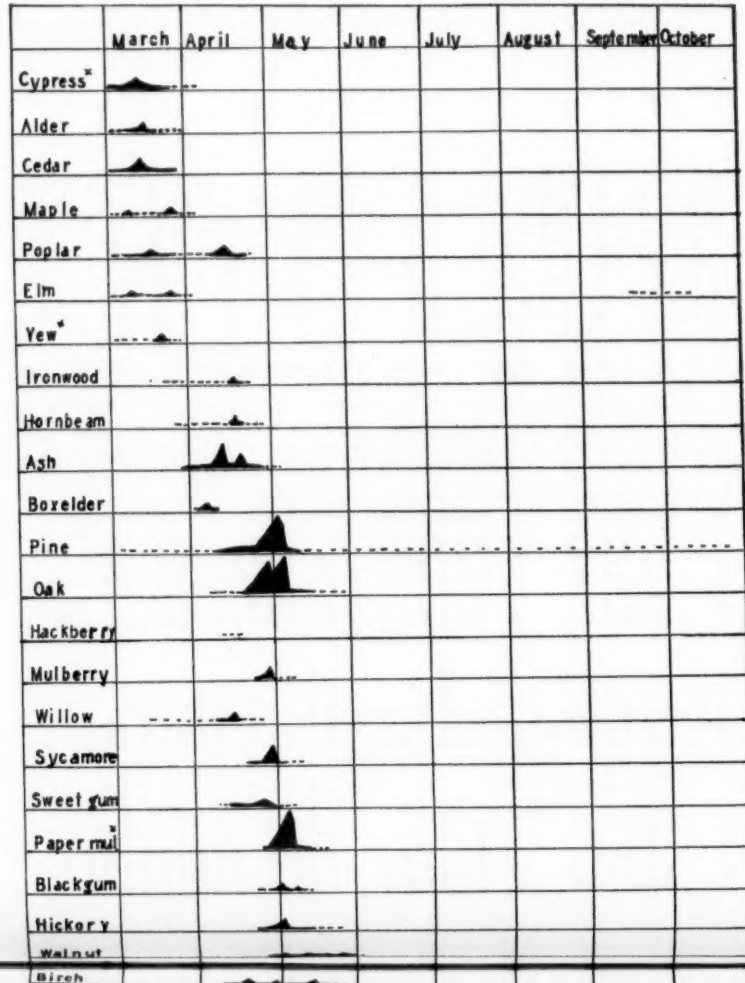
TABLE II

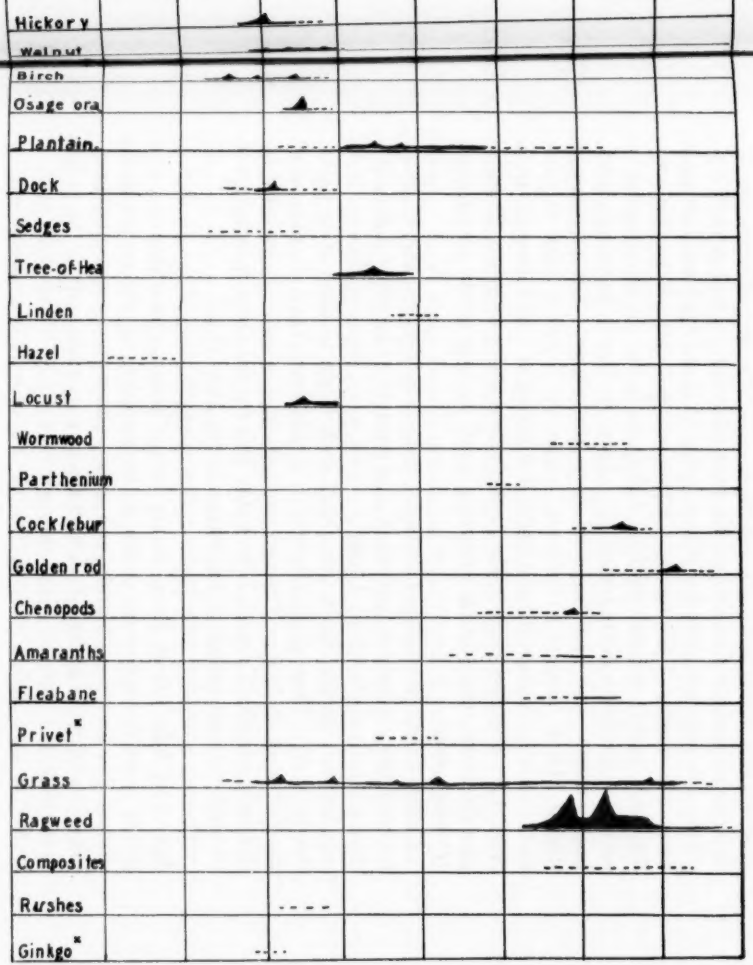
Common grasses and wind pollinated weeds of Albemarle County

COMMON NAME	BOTANICAL NAME	BLOOMING DATE
	Grasses	
Barnyard grass	*Echinochloa crus-galli*	July–September
Bent grass	*Agrostis alba*	June–July
Blue grass	*Poa pratensis*	June
Broom sedge	*Andropogon*	July–August
Crab grass	*Digitaria sanguinalis*	July–September
Cheat	*Bromus secalinus*	June–July
Darnel	*Lolium temulentum*	June–July
Fescue	*Festuca*	June–July
Foxtail	*Setaria glauca*	July–August
Goose grass	*Eleusine indica*	June–September
Johnson grass	*Sorghum halepense*	June–July
Oat grass	*Danthonia spicata*	June
Orchard grass	*Dactylis glomerata*	June
Poverty grass	*Aristida dichotoma*	August–September
Panic grass	*Panicum*	July–August
Rye grass	*Lolium perenne*	June–July
Sweet vernal	*Anthoxanthum odoratum*	May–June
Timothy	*Phleum pratense*	June
Tall red top	*Tridens flavus*	August–September
	Weeds	
Burdock	*Arctium Lappa*	August–October
Cocklebur	*Xanthium*	August–September
Dock, broad leaf	*Rumex obtusifolius*	July–August
Dock, narrow leaf	*R. crispus*	July–September
Goose foot	*Chenopodium glaucum*	August–September
Wormseed	*C. ambrosioides*	August–September
Nettle	*Urtica*	July–September
Lamb's quarters	*Chenopodium album*	August–September
Pigweed, red root	*Amaranthus retroflexus*	August–September
Plantain, broad leaf	*Plantago major*	May–September
Plantain, narrow leaf	*P. lanceolata*	April–September
Ragweed, dwarf	*Ambrosia artemisiifolia*	August–October
Ragweed, giant	*A. trifida*	August–October
Sheep sorrel	*Rumex acetosella*	May–July
Spiny amaranth	*Amaranthus spinosus*	August–September
Tumble weed	*A. graecizans*	July–September
Wormwood	*Artemisia*	August–September

TABLE III

COMMON NAME	BOTANICAL NAME	DATE OF POLLINATION	DATE OF MAXIMUM CONCENTRATION PER CU. YD.	MAXIMUM CONCEN. PER CU. YD.	REMARKS
Maple	*Acer*	Mar. 1–Apr. 3	Mar. 14–Mar. 24	122	Some pollen of these genera was caught as early as Jan. 18
Alder	*Alnus*	Mar. 3–Mar. 30	Mar. 14	135	
Red Cedar	*Juniperus virginiana*	Feb. 28–Mar. 23	Mar. 14	215	
Cypress	*Taxodium distichum*	Mar. 3–Apr. 4	Mar. 14	360	Cypress is rare, but there are several trees nearby
Poplar	*Populus*	Mar. 3–Apr. 20	Mar. 18	70	Two species
			Apr. 15	130	
Elm	*Ulmus*	Mar. 3–Apr. 4	Mar. 9	60	Pollen of a fall species was caught during Sept. and Oct.
			Mar. 14	66	
Yew	*Taxus*	Mar. 9–Mar. 25	Mar. 18	40	Cultivated
Ironwood	*Carpinus*	Mar. 25–Apr. 24	Apr. 20	16	
Hornbeam	*Ostrya*	Mar. 28–Apr. 26	Apr. 20	20	
Ash	*Fraxinus*	Mar. 28–May 2	Apr. 11	700	Ash is abundant nearby
Boxelder	*Acer Negundo*	Apr. 4–Apr. 10	Apr. 8	36	
Pine	*Pinus*	Apr. 10–May 10	May 2	960	Some pine pollen was caught throughout the year
Oak	*Quercus*	Apr. 12–May 30	Apr. 28	814	
			May 4	994	
Hackberry	*Celtis*	Apr. 10–Apr. 14	Apr. 9	6	Rare
Willow	*Salix*	Mar. 14–Apr. 20	Apr. 14	116	
Sweet gum	*Liquidambar*	Apr. 12–Apr. 30	Apr. 25	65	Rare
Hazel	*Corylus*	Mar. 2–Mar. 30	Mar. 14	7	
Mulberry	*Morus*	Apr. 24–May 6	Apr. 26	120	
Birch	*Betula*	Apr. 10–May 15	Apr. 14		
			Apr. 26	40	
			May 12		
Sycamore	*Platanus*	Apr. 20–May 4	Apr. 27	210	
Paper mulberry	*Broussonetia*	Apr. 25–May 15	May 4	1020	Common as an escape
Black gum	*Nyssa*	Apr. 25–May 9	May 1	50	
Hickory	*Carya*	Apr. 26–May 15	May 2	160	
Walnut	*Juglans*	Apr. 26–May 31	May 2	66	
Spruce	*Picea*	Apr. 25–May 5	May 1	70	Cultivated
Beech	*Fagus*	Apr. 25–May 10	May 2	9	
Plantain	*Plantago*	May 10–Sept. 8	June 14	38	
Osage orange	*Maclura*	May 10–May 16	May 13	216	
Sedges	*Cyperaceae*	Apr. 10–May 15			Only occasional grains
Dock	*Rumex*	Apr. 20–May 31	May 4	58	
Tree-of-Heaven	*Ailanthus*	May 28–June 25	June 14	70	Common nearby
Linden	*Tilia*	June 20–July 8	June 29	5	
Locust	*Gleditsia*	May 10–May 27	May 13	40	
Grass	*Gramineae*	Apr. 15–Oct. 15	May 8		
			May 26		
			June 20	60	
			July 10		
			Sept. 25		
Privet	*Ligustrum*	June 14–July 5	June 25	5	Cultivated
Rushes	*Juncus*	May 10–May 24	May 3	2	
Ginkgo	*Ginkgo*	Apr. 29–May 5	May 2	5	Cultivated
Chenopods	*Chenopodium*	July 26–Sept. 3	Aug. 27	10	
Amaranths	*Amaranthus*	July 12–Sept. 10	Aug. 28	6	
Wormwood	*Artemisia*	Aug. 20–Sept. 18	Sept. 5	5	
Fleabane	*Erigeron*	Aug. 12–Sept. 14	Sept. 4	4	
Ragweed	*Ambrosia*	Aug. 12–Oct. 30	Aug. 22	860	
			Sept. 5	1020	
Parthenium	*Parthenium*	July 28–Aug. 7	Aug. 4	2	
Goldenrod	*Solidago*	Sept. 10–Oct. 8	Sept. 29	14	
Composites	*Compositae*	Aug. 15–Oct. 10	Sept. 29	5	
Cocklebur	*Xanthium*	Sept. 1–Sept. 28	Sept. 16	25	


March
April
May
June
July
August
September
October
Cypress*
Alder
Cedar
Maple
Poplar
Elm
Yew*
Ironwood
Hornbeam
Ash
Boxelder
Pine
Oak
Hackberry
Mulberry
Willow
Sycamore
Sweet gum
Paper mul*
Blackgum
Hickory
Walnut
Birch



x Planted or escaped

CHART 1

the grains recorded during November, December, January, and February were mostly relics of the previous season left in the dust, and were not sufficiently abundant to be reckoned with.

Although pollen of early blooming trees occurred spasmodically during warm spells in February, it was not present in sufficient concentration to be important until March 3. On this date cypress, poplar, elm, alder, hazel, cedar, and maple were recorded. These genera constitute the principal flora for March, most of them reaching their peak about the middle of the month. Cypress is not endemic to this area. The high pollen concentration of this genus is due to the presence of several large trees planted close by. Later in March ironwood, hornbeam, willow, and pine begin to occur irregularly. The pine caught during March appears to be fresh, and very probably blew in from farther south, as pines did not begin pollinating at Charlottesville until April 12. The first peak in the poplar curve is due to aspen (*Populus grandidentata*), the second, occurring April 15, represents cottonwood (*Populus alba*).

Cottonwood, ironwood, hornbeam, ash, boxelder, hackberry, mulberry, willow, sycamore, and sweet gum reach their height of pollination during April, as shown by Chart 1. Oak, pine, paper mulberry, hickory, walnut, spruce, black gum, and dock begin to shed their pollen late in April. These genera, however, do not reach their maxima until the first week in May. The two-pointed curve of oak is occasioned by different species, the same is probably true for the three-pointed curve of birch. Osage orange is important about May 15.

There is a decided drop in the pollen concentration of the air during June and July. Only three woody forms, linden, tree-of-heaven, and privet, contribute enough pollen to be recorded on the pollen slides during this period. Plantain and grass, although never contributing large quantities of pollen, do constitute an important part of the pollen flora from the first of May through September. The low concentration of grass pollen is not indicative of a scarcity of grasses, for they are abundant, but is caused by the lowness of the plants and the relatively large size of the pollen grains. The numerous peaks in the grass curve are obviously caused by different blooming dates of various species.

On August 12, seventeen ragweed pollen grains were caught on a single slide. This was sufficient number to indicate that ragweed was actually blooming in the neighborhood. These seventeen grains were identified as giant ragweed (*A. trifida*). The concentration of ragweed

pollen increased rapidly to August 22, when it reached 860 grains per cubic yard. After this date there was a decrease of pollen until September 2, then it began to rise and finally reached the maximum of 1020 grains per cubic yard on September 5. This peak was followed by a sharp decline to 220 grains per cubic yard on September 12, then the count remained more or less constant until September 25. A gradual diminution of ragweed continued until late October, when concentration became so low that it was evident that the ragweed season was over.

Wormwood, golden rod, chenopods, amaranths, fleabane, and unidentified composites are recorded in the chart and Table III. Their concentration never reaches magnitudes sufficient to be considered important, however.

DISCUSSION

The old question of "what pollen concentration of the air is necessary to excite hayfever symptoms in sensitive individuals" remains unsettled. Blackley (5) in 1873 concluded that 25 pollen granules inhaled per day were sufficient to cause hayfever. Durham (6) states: "Some ragweed-sensitive persons begin to sneeze by the time the first pollen grains appear in the air. Others do not begin until the air contains ten, twenty, or fifty pollen grains per cubic yard. The inhalation of twenty-five granules of pollen in a day's time is usually sufficient to cause trouble. This is a very small amount when it is remembered that there are billions of ragweed pollen grains in an ounce of pollen. Positive skin tests have been obtained by injecting into the skin the extract of one-tenth of a granule of ragweed pollen" (pp. 132, 133). He does not state here how he arrived at the pollen concentration, though earlier in his book he says that he used Scheppegrell's formula $n = 1.8N$. Since this formula has been proved to be incorrect (Cocke, 2), his estimate of the pollen concentration necessary to excite symptoms may be too low. The same may be true for the estimate given by Feinberg and Steinberg (7) of 25 grains per cubic yard.

Brown (8) is of the opinion that unless pollen applied to the nasal mucous membrane is much more active in producing symptoms than the same amount injected subcutaneously, or else that pollen inhaled from the air has a cumulative effect on the system, the atmospheric pollen concentration necessary to cause hayfever is generally greatly underestimated. Brown makes the following statement:

"Durham (6) has estimated that if a patient were out of doors standing by the pollen slide during the whole twenty-four hours, the maximum

amount he would inhale on the worst day we have had in Washington would be about 4,000 granules. This is allowing 20 cubic yards of air for the twenty-four-hour intake, and multiplying this by the average number of pollen granules per cubic yard of air for the period. This total of 4,000 granules inhaled would represent 8 pollen units, so that the maximum contact in Washington would be only 8 units per day.

"Patients who have worked up to doses of 50,000 or more pollen units, and are taking increases of 5,000 to 10,000 units at a time, certainly would not be affected by an increment of only 8 units. Furthermore, it is the exceptional patient indeed who has any symptoms from a dose of 8 pollen units injected out of season.

"I can think of only three possible explanations for this marked discrepancy. The first and most likely one would be that the estimates as to the amount of pollen inhaled from the air are grossly erroneous. The second explanation would be that 8 units of pollen applied to the nasal mucous membrane is much worse than 8 pollen units injected subcutaneously. The final explanation would be that the pollen inhaled from the air has a cumulative effect in the system."

I have already shown in two previous papers (Cocke, 2, 3) that Brown's first assumption explaining this discrepancy is correct, that is, earlier methods of estimating the pollen concentration per cubic yard have been grossly erroneous. However, the method used in this paper for determining the pollen concentration of the air has been proved both by theory and actual experiment to be approximately correct. But even with the greater concentration of pollen per cubic yard which the present method gives over Scheppegrell's formula ($n = 1.8N$), there is still a discrepancy existing between the amount of pollen which produces ill effects when breathed as compared with the subcutaneous dose which gives a positive reaction. This fact can be explained, I think, only by Brown's last two assumptions—that is, first, pollen is much more toxic when inhaled than when injected subcutaneously, and, second, pollen inhaled from the atmosphere has a cumulative effect on the system which produces serious effect even when inhaled in minute quantities.

LITERATURE CITED

1. NEFF, A. H. The native trees of Albemarle. Thesis for M. A. Degree, University of Virginia, 1927.
2. COCKE, ELTON C. Calculating pollen concentration of the air. J. Allergy **8**: 601-606. 1937.
3. ——— Method for determining the pollen concentration of the air. J. Allergy. In press.

4. SCHEPPEGRELL, WM. Hayfever and asthma. Lea and Febiger. New York. 1922.
5. BLACKLEY, C. H. Experimental research on the cause and nature of *Catarrhus Aestivus*. London. 1873.
6. DUNHAM, O. C. Your hayfever. The Bobbs-Merrill Co., New York. 1936.
7. FEINBERG, S. M., AND M. J. STEINBERG. Studies on pollen potency. J. Allergy **5**: 19. 1933.
8. BROWN, G. T. Further experiences with maximum dosage pollen therapy. J. Allergy **6**: 86–92. 1934.

OBSERVATIONS ON THE DEVELOPMENT OF A NEW SPECIES OF PHYTOPHTHORA*

By Leland Shanor

Plates 15 and 16

While examining for aquatic Phycomycetes some water collections made in high altitude pools in the vicinity of Highlands, N. C., a species of *Phytophthora* growing on the petals of *Rhododendron maximum* which had fallen into a small spring stream was isolated. The spiny nature of the oogonia of this plant immediately attracted the attention of the author as he could not recall having seen any literature on or figures of a species with oogonia of this character. Jones *et al* (1912) had figured resting bodies of *P. infestans* which resemble the oogonia of the present fungus only in their spiny character. The resting bodies figured and described by these authors lacked antheridia and are considered a type of chlamydospore. They could not be considered organs of sexual reproduction.

Wilson, in 1914, reviewed the then known species of *Phytophthora*, basing his taxonomy upon morphological characters and hosts. Rosenbaum (1917) attempted to set up a criterion for species in this genus, using a biometrical scheme based upon spore and sporangial measurements. Leonian (1925, 1934) and Leonian and Geer (1929) have worked out a classification of *Phytophthora* based chiefly upon a physiological separation of species—species that morphologically are often very similar. Leonian and Geer place no confidence in a morphological method of separating species because the size of the sporangia of different strains of the same species often present great variation under uncontrolled cultural conditions. As cultural conditions and hosts are altered (Leonian, 1927), so are the sizes of sporangia. Tucker (1931),

* This plant was found while the writer was working on a research scholarship granted by the University of North Carolina to study at the Samuel T. Weyman Laboratory, Highlands, N. C., and the investigation was completed in the Botanical Laboratory of the University of North Carolina. He is grateful to Dr. W. C. Coker and Dr. J. N. Couch for helpful suggestions and constructive criticism.

after a careful study of the genus, gives a key for separation and identification of 19 species and one variety. In a later publication (1933) he has compiled a comprehensive bibliography relating to the distribution of the genus. Leonian (1934), after further studies on *Phytophthora*, believes that the genus contains only three good species, namely, *Phytophthora cactorum*, *P. infestans*, and *P. palmivora*. He has, however, given a key whereby 22 species and varieties can be identified.

So far as I have been able to determine there are no known species of *Phytophthora* that have spiny oogonia, and this species is therefore distinct from all others in possessing this characteristic. Since this species has very sharp, gradually tapering spines, the author has selected the name *Phytophthora stellata* as appropriate. The description follows:

Phytophthora stellata n. sp.

Growth delicate on Rhododendron petals and on hemp seed in water, quite dense and often reaching out to a length of 1–2 cm. or more. Threads of the mycelium 3.5–7.0μ thick, mostly about 5.6μ, very rarely septate; septa, when present, found near reproductive branches or in old cultures. Walls giving a cellulose reaction with chloroiodide of zinc. Sporangia borne either terminally or on short lateral branches, usually somewhat obpyriform, sometimes more oval or more elongated; if terminal measuring from 80.6–115.8μ long by 36μ wide, mostly about 86.6 x 36μ, if lateral 28.6–61.8μ by 21.7 to 26.9μ, mostly about 44.25 x 26.9μ. Zoospore formation and sporangium development are of the *P. palmivora* type and a vesicle is usually formed at the end of an exit tube. Zoospores biciliate, spherical to reniform and measuring 10.3 to 14.4μ when resting. Oogonia borne on short side branches, spherical, 15.5–22.4μ in diameter, occasionally up to 30μ, with sharp spines of various lengths, measuring up to 3.6μ long. Eggs single, almost filling the oogonium, measuring 13.8μ to 17.2μ, mostly about 14.3μ to 15.5μ. The walls of young oogonia present a yellowish brown color, becoming more hyaline at maturity. Mature eggs have a single large eccentric oil globule. Antheridial branches arise either from the same or adjoining hyphae to the oogonium, but most often arise only a short distance below the oogonium. Antheridia single, club-shaped, much larger than the antheridial branch, 7.0–10.4μ thick. The antheridium is most frequently attached near the stalk. Because of its position, the oogonium often appears to have grown up through the antheridium. The contents of the antheridium are emptied into the oogonium and antheridia attached to mature eggs are entirely empty.

Collected once on petals of *Rhododendron maximum* which had fallen into a cold spring in front of Mr. Mell's cabin near Highlands, North Carolina, in August, 1937.

Rosenbaum (1917) in working out his classification of the genus, separated the species into three groups according to the type of antheridium present. In his first group, the *cactorum* group, the antheridium is said to be attached to the side of the oogonium (paragynous). In his second group, the *phaseoli* group, the antheridium is said to be attached at the base of the oogonium (amphigynous). The oogonium in this group is thought to grow up through the antheridium and then develop, leaving the antheridium as a collar around its base. Since Pethybridge (1913) demonstrated this phenomenon, it has been shown for several species by other workers and has been supported by the cytological investigation of Murphy (1918). In his third group, the *faberi* group, Rosenbaum places all species in which antheridia are unknown.

There seems to be some disagreement as to the accuracy in placing some species either in the *cactorum* group or the *phaseoli* group. *Phytophthora cactorum*, for instance, has been shown to possess both paragynous and amphigynous antheridia. The question has also been raised by Fitzpatrick (1930) as to whether oogonia in the *cactorum* group actually grow up through antheridia, or whether the antheridium is found in a basal position because it coils around the base of the oogonium as has been shown by Cooper (1928) and by Cooper and Porter (1928). Cooper has studied *P. cactorum*, *P. erythroseptica*, *P. richardiae*, and *P. terrestris* in addition to *P. paeonae* and has found this to be the case for all of these species. Earlier investigations on some of these same species and on several others had led to the belief that the oogonium grew up through the antheridium, and although this phenomenon was very unusual, it had been accepted. Observations on *P. stellata* substantiate the observations of Cooper and it is possible that more detailed studies on the early development of other members of this genus will show that the antheridium coils about the base of the oogonium rather than the latter growing up through it.

Most antheridia of *P. stellata* upon first examination appear to be of the amphigynous type, but careful focusing and study with good optics reveal the fact that antheridia in this species coil around the base of the oogonia as is often the case in *P. paeoniae*. Careful study of developing stages bear this out very clearly.

THE DEVELOPMENT OF THE SEXUAL ORGANS OF *P. stellata*

For the study of the development of the sexual organs of this fungus, cultures grown on hempseed in distilled water and cultures growing

on maltose-peptone agar #5 were used. The course of development on either medium was identical. The oogonia, when developing in water on hempseed cultures, possess longer and more pointed spines than do those produced in the agar. Those in agar are also slightly larger and the antheridium is smaller than those produced in water. Development was followed both in agar and in water on hempseed, but most of the figures were made from agar cultures. Development in water was terminated if a cover glass were placed over the culture, so it was more difficult to get a good series of developmental stages for figures from these cultures.

The earliest stages in the development that can be recognized are short side branches that have parted so that the two branches appear of about equal length. The one branch seems to grow slightly more rapidly than the other. After growing a short distance, these two branches approach each other. Sometimes they just come in contact but more commonly the one tends to coil around the other (fig. 12) and then soon enlarges (figs. 1 and 13). This branch that coils around the other and enlarges first is destined to form the antheridium. The development of the antheridium in this species seems always to precede slightly the development of the oogonium. The oogonium does not enlarge until after the attachment of the antheridium has taken place. Figs. 2, 6, and 14 show young stages in the early development of oogonia. The protoplasm in the threads and in the young reproductive branches contains many small refractive oil globules.

Sometimes the primary reproductive branches do not grow toward each other but put out secondary branches that come together and develop into antheridia and oogonia (fig. 2). This type of development, as shown in fig. 2, resembles slightly some figures of early stages in development of members of the *erythroseptica* group. In figure 2 it is clear, however, that the antheridium coils around the young oogonial initial rather than the latter growing up through the antheridium. Figures 4, 5, 6, 7, and 15 show early stages in the development of sexual organs and show clearly that the antheridium is coiled about the base of the developing oogonium.

As the antheridium and oogonium develop the protoplasm flows into them, particularly into the oogonium, and appears quite dense and somewhat foamy. As the oogonium approaches its mature size, protuberances grow out at various places over its surface (figs. 8, 9, 16, and 17). The walls of these are at first very thin and the cytoplasm in them is more hyaline and much less granular than that occupying the

central part of the oogonium (figs. 17, 18). These protuberances continue to elongate and become the spines on the wall. In water cultures these spines become very sharp-pointed, but in agar cultures they seldom have such sharp apices.

As the spines are developing on the oogonium, the protoplasm in the center of the oogonium seems to shift position slightly from time to time. These changes in position seem to have no significance. At times more hyaline cytoplasm appears to surround the more densely granular protoplasm. By the time the spines have reached their full length, a thin membrane has formed around the more dense protoplasm of the oogonium (fig. 19) and the antheridium has previously been cut off from the antheridial branch by a cross wall (figs. 18 & 19). In this condition, after the thin membrane is formed around it, the young oosphere is ready for fertilization. Young oospheres commonly lie close to the oogonial wall just opposite the antheridium (figs. 19, 20, and 21).

A very short fertilization tube now grows in from the antheridium and presses against the oosphere membrane. Finally the membrane ruptures and the antheridium discharges its contents into the oogonium. If the antheridium and oogonium are in a median focal plane, a path through the cytoplasm of the young oosphere from the end of the fertilization tube toward its center can be detected (fig. 23). This stage is hard to find as oogonia and antheridia in the correct relationship for this observation are scarce. Of the many developing oogonia watched, I was able to detect this faint fertilization path only three times. Usually all of the antheridial contents pass into the oogonium, but sometimes a few granules are left behind and disintegrate (figs. 24, 20, 21, 25, and 26).

After fertilization the oosphere forms a wall about itself. This wall in the mature condition is made up of two layers of about equal thickness. As the wall is forming, the small oil globules in the oosphere begin to coalesce to form larger oil globules (figs. 20 and 24). These finally all unite into a single slightly eccentrically placed oil globule (figs. 21, 25, 26), a condition characteristic of mature eggs. Germination of the eggs has not been observed.

SPORANGIAL DEVELOPMENT

It was difficult for some time to get many sporangia to complete their development and liberate zoospores at ordinary laboratory temperature (77°F.). It was then suggested that young cultures might mature

sporangia if placed in the ice box where the temperature would be somewhat lower (48°F.). Under these conditions sporangial development was normal and often cultures containing developing sporangia when placed in the ice box could be found liberating zoospores after being in the ice box from one and one-half to two hours. When cultures were taken out to be examined, zoospore formation would be retarded after a short time at room temperature, but continued spore formation could be brought about by placing cultures back in the ice box. Sometimes as short a time as fifteen minutes back in the ice box would be sufficient to bring about normal sporangial development again. Sporangia formed at room temperature go into a dormant condition and are characterized by having one or more large oil globules (figs. 30, 31). Sporangia may remain in this condition for several days or longer. If cultures containing resting sporangia are placed in the ice box over night, many sporangia can be found in the morning developing normally and liberating zoospores.

Sporangia of this species are typically obpyriform in shape and may be borne either terminally or on short side branches (fig. 27). The terminal sporangia are considerably larger than the ones borne on lateral branches and are more elongated (figs. 27, 29, 30, 31, 32). The course of sporangial development is of the type described by Butler (1907) for *Phytophthora* (*Pythium*) *palmivora* and in some cases very closely approaches the course of spore liberation and development found in the genus *Pythium*. Forms in which the sporangial contents have been freed into a vesicle entirely undifferentiated and forms in which the zoospores are liberated into the vesicle almost completely formed have been observed.

The stages in the development of the sporangium and the formation of the zoospores are so nearly identical with similar stages figured by Butler (1907) for *P. palmivora* and by Rosenbaum (1917) for *P. arecae* that a detailed account for this species seems unnecessary. Figures 28, 35, 36, 37, 38, show stages in spore formation and escape. In this species a cylindrical exit tube is produced and at the end of this tube the vesicle is formed (fig. 38). This tube may be several microns long or be almost entirely absent. Zoospores are reniform to spherical in shape and measure 10.3–14.4μ long. The zoospores possess two cilia of about equal length, which are attached laterally at the hilum (fig. 39).

Sporangia that do not mature zoospores often germinate to form secondary sporangia. This is particularly true in the case of young sporangia when environmental conditions have been altered before the

septum has been formed. After spores have been liberated, proliferation of new sporangia from the base of the old sporangia often takes place. A secondary sporangium has never been observed within the first, but the secondary sporangium is formed at the end of a long stalk which grows out through the exit tube of the old sporangium (fig. 34).

TAXONOMIC CONSIDERATIONS

Fitzpatrick (1923, 1930) has shown that the line of demarcation between the genera *Pythium* and *Phytophthora* is very questionable and he suggests that perhaps further investigations of these genera will result in the combining of the two. De Bary (1876), in establishing the genus *Phytophthora*, realized the close affinity of this genus to *Pythium*, but separated the two on their slightly different methods of sporangial germination. In *Pythium*, Butler (1907), Matthews (1931) and others consider that the zoospores are regularly formed in a vesicle, while in *Phytophthora* they are thought to be fully formed within the original sporangium, even in cases when they are emptied into a vesicle. It has been shown that there is no clearly cut distinction between the method of sporangial germination in the two genera (Butler, 1907, and Rosenbaum, 1917), and that in *Phytophthora* sporangial germination typical of *Pythium* occurs. Fitzpatrick (1930) says: "The shape of the sporangium in most species of *Pythium* may be said to be characteristically more nearly spherical than in *Phytophthora* where it is usually oval to obpyriform and papillate, but so many integrating conditions exist that shape has only relative diagnostic value. Buisman summarizes the situation with the statement that although theoretically no sharp line can be drawn between the two genera, it is usually possible in practice to determine whether a given form belongs to the *Phytophthora* type or to the *Pythium* type."

In deciding whether the present plant was a *Pythium* or a *Phytophthora*, the author realized the fact that often the type of sporangial development strongly suggests *Pythium*, but felt that the shape of the sporangia and the presence of a papilla indicated that it was a *Phytophthora* whose sporangial germination shows a close relationship to *Phytophthora palmivora* Butler. Butler (1907) at first considered *P. palmivora* as *Pythium palmivorum*, but later concluded that his plant was a *Phytophthora* (Sharples and Lambourne, 1922).

SUMMARY

1. A new species of *Phytophthora* with spiny oogonia is described and named *P. stellata*.

2. The development of the sexual organs of this species is discussed and a comparison is made with methods known for other members of the genus.

3. Sporangial development and zoospore formation are considered and compared with that of other species of *Phytophthora* and with *Pythium*.

4. The taxonomic relationships of this species are brought out and in its sporangial development this species is shown to be closely related to *P. palmivora* Butler.

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LITERATURE CITED

1. BARY, ANTON DE. 1876. Researches into the nature of the Potato fungus, Phytophthora infestans. Journ. Roy. Agric. Soc., England, Ser. 2, **12**: 239–269.
2. BUTLER, E. J. 1907. An account of the genus Pythium and some Chytridiaceae. Mem. Dept. Agric. India, Bot. Ser. **1**: 1–160.
3. COOPER, DELMER. 1928. Paragynous antheridia of Phytophthora spp. Phytopathology **18**: 149.
4. ——— AND PORTER, C. L. 1928. Phytophthora blight of peony. Phytopathology **18**: 881–899.
5. FITZPATRICK, H. M. 1923. Generic concepts in the Pythiaceae and Blastocladiaceae. Mycologia **15**: 166–173.
6. ——— 1930. The Lower Fungi. Phycomycetes. McGraw-Hill Book Co., Inc.
7. JONES, L. R., GIDDINGS, N. J., AND LUTMAN, B. F. 1912. Investigations of the potato fungus, Phytophthora infestans. U. S. Dept. Agric. Bur. Plant Indus. Bull. **245**: 100.
8. LEONIAN, L. H. 1925. Physiological studies on the genus Phytophthora. Amer. Jour. Bot. **12**: 444–498.
9. ——— 1927. The effect of different hosts upon the sporangia of some Phytophthoras. Phytopathology **17**: 483–490.
10. ——— 1934. Identification of Phytophthora species. West Virg. Agric. Exp. Station Bull. **262**: 2–36.
11. ——— AND GEER, H. L. 1929. Comparative value of the size of Phytophthora sporangia obtained under standard conditions. Jour. Agr. Res. **39**: 293–311.
12. MATTHEWS, V. D. 1931. Studies on the Genus Pythium. Univ. of N. C. Press, Chapel Hill, N. C.
13. MURPHY, P. A. 1918. The morphology and cytology of the sexual organs of Phytophthora erythroseptica. Ann. Bot. **32**: 115–153.

14. PETHYBRIDGE, G. H. 1913. On the rotting of potato tubers by a new species of Phytophthora having a method of sexual reproduction hitherto undescribed. Sci. Proc. Roy. Dublin Soc. **13:** 529–565.
15. ROSENBAUM, J. 1917. Studies of the genus Phytophthora. Journ. Agr. Res. **8:** 233–276.
16. SHARPLES, A., AND LAMBOURNE, J. 1922. Observations in Malaya on Bud-rot of Coconuts. Ann. Bot. **36:** 55–70.
17. TUCKER, C. M. 1931. The Taxonomy of the Genus Phytophthora. Mo. Agric. Exp. Sta. Res. Bull. 153, 208 pp.
18. ——— 1933. The distribution of the genus Phytophthora. Mo. Agric. Exp. Sta. Res. Bull. 184, pp. 1–80.
19. WILSON, GUY WEST. 1914. Studies in North American Peronosporales V. Mycologia **6:** 54–83.

EXPLANATION OF PLATES

PLATE 15

Figs. 1–9. Early stages in development of antheridia and oogonia. Figs. 1–5 from agar cultures; 6–9 from water cultures growing on hemp seed. ×505.

Figs. 10 & 11. Surface views of two reproductive branches showing general appearance. Fig. 10 from water culture; fig. 11 from agar culture. ×505.

Figs. 12–21. Stages in development of sexual organs. Fertilization took place between 19 & 20. The contents of antheridium could not be followed because of the position of the organs but a gradual decrease in antheridial contents could be observed. From an agar culture. ×505.

Figs. 22–24. Stages in fertilization. Fig. 22 shows penetration of fertilization tube through oogonial wall and pressing against oosphere membrane. Fig. 23, a median optical section showing the contents of antheridium passing into oosphere and through oosphere cytoplasm. Faint indications of an ooplasm and a periplasm can be seen in the oosphere. Fig. 24 shows a little later stage in which a wall is forming and a few protoplasmic granules can be seen disintegrating in the antheridium. ×830.

Figs. 25–26. Mature eggs in oogonia from water cultures. ×505.

PLATE 16

Fig. 27. Habit sketch of a portion of a hypha showing numerous sporangia and a reproductive branch. ×83.

Fig. 28. Early stage in formation of a sporangium. ×367.

Figs. 29–31. Terminal sporangia. Figs. 30 & 31 resting conditions showing large oil globules. ×367.

Figs. 32–33. Lateral sporangia; fig. 33 forming exit tube previous to spore formation. ×367.

Fig. 34. Showing proliberation of a second sporangia from base of older empty one. ×175.

Fig. 35. Empty sporangium showing exit tube. ×367.

Figs. 36–38. Stages in sporangial germination.

Fig. 39. Zoospores, (a) resting condition. ×367.

PLATE 15

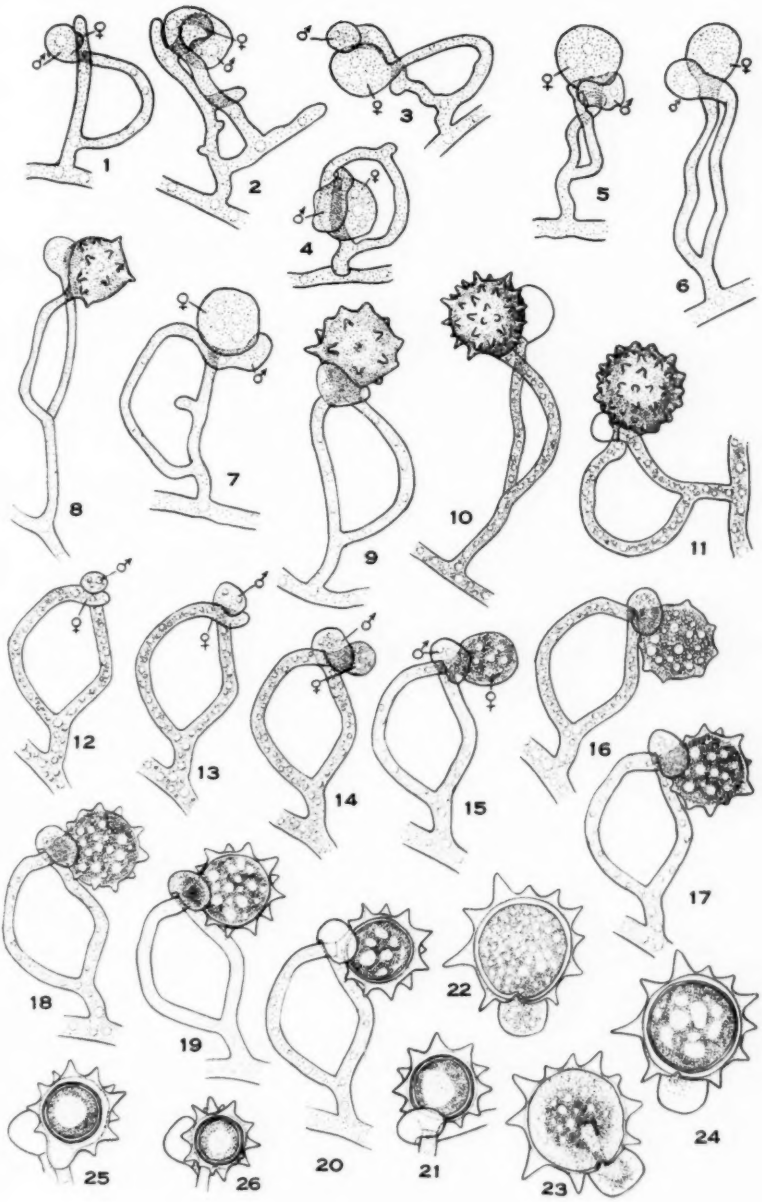

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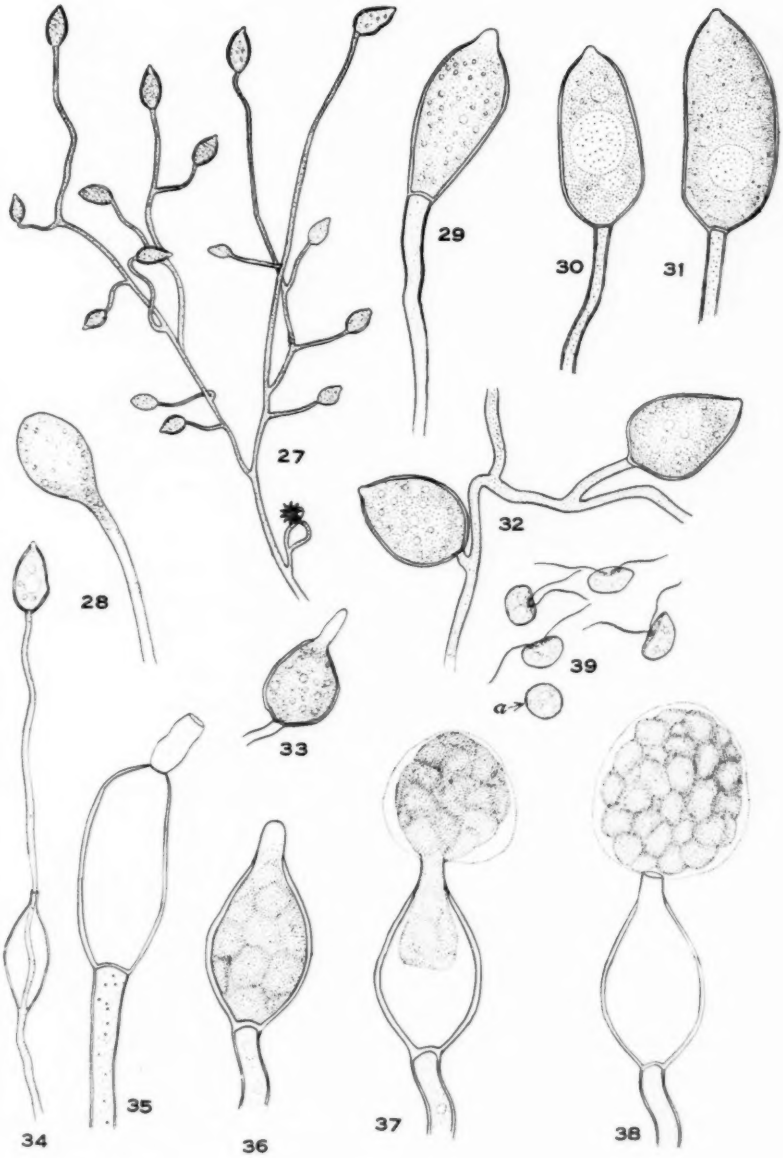
PLATE 16



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